The interaction between a keystone plant species and its dominant epiphyte on Marion Island: climate change implications

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Declaration:

I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature…….. Date…….

This work is dedicated to my mother, **Nogusha Florette Buwa** and to my sisters, **Kholiswa** and **Nolwazi Buwa**. You all inspire me, ndinithanda kakhulu ma-lady…

Abstract

Climate has shown some remarkable changes over the past century, especially at the polar and sub-polar regions. Southern Ocean Islands provide good models for studies related to climate change effects, since effects may be evident in the short term and may also be clearer. Marion Island is an example of such a system with a harsh abiotic environment, and low species richness often vulnerable to change. Climate change is predicted, and also reported, to have biological consequences on plant communities, affecting the phenology, morphology, and the interaction between individuals and species. This study examines the association between the keystone plant species, *Azorella selago* Hook. (Apiaceace), and its dominant epiphyte *Agrostis magellanica* Lam. (Poaceae). Two complimentary approaches were used, one observational and the other experimental. The main objective for the observational study was to quantify biotically-relevant microclimate temperature, as well as the morphology, epiphyte load and phenology of *A. selago* at three different altitude sites on Marion Island. This provided information on baseline variation for understanding specific variability in plant response to the experimental part of this study, against which future patterns arising from biological monitoring can be compared. Studying plants at different altitudes provides a possible analogue for temperature-related climate change consequences for the ecology of *A. selago*, and its interaction with *A. magellanica*. The microclimate temperature associated with *A. selago* differed between the three sites examined. This difference was related to local topographic conditions and altitude differences. Cushion size differed distinctively between the three altitude sites, with this difference related to environmental heterogeneity such as differences in age and substrate structure. *Azorella selago* annual growth rate was estimated through stem length and the number of leaves on both exposed and shaded stems. Within-site variability, as well as epiphyte cover were found to be the contributing factors on *A. selago* annual growth rate. This highlights the importance of site-specificity when estimating growth rate within and between different altitude sites. Leaf characteristics differed between the sites, with this attributed to local habitat conditions, such as topography, as well as epiphyte cover. As expected, the difference in leaf size between exposed and shaded leaves demonstrated a larger specific leaf area on

leaves shaded by *A. magellanica*. *Agrostis magellanica* abundance and density were altitudinally related, with *A. selago* demonstrating facilitation effects on *A. magellanica*. The trend shown in this study suggests that in spite of general facilitative effect of *A. selago* on *A. magellanica* towards higher altitudes, the abiotic environmental threshold for *A. magellanica* occurs at lower altitudes than it does for *A. selago*. Phenological differences were also apparent between the three sites. The objectives of the experimental part of this study were to quantify the effect of the dominant epiphyte, *A. magellanica* on biotically-relevant microclimatic temperatures, as well as on the phenology and physical condition of *A. selago*. Different treatments were applied to cushions at the three altitude sites to examine the shading effect of epiphytic *A. magellanica* on cushion plants, as well as the effect of treatment-related disturbance. *Azorella selago* microclimate temperature showed no significant difference between treatments, suggesting that on average epiphytic *A. magellanica* cover has no effect on cushion microclimate temperature. The percentage of flower budding and flowering of *A. selago* was negatively related to epiphyte cover. Cushion vitality was also responsive to epiphyte cover, with higher vitality scores on low grass covered cushions than on high grass cushions. This shows that *A. magellanica* competes with *A. selago*, while *A. selago* facilitates *A. magellanica*. Heavy epiphyte numbers impose negative effects on *A. selago* vegetative and reproductive performance, as well as cushion vitality. Therefore, the results of this research show that the vegetative and reproductive performance of *A. selago* and cushion vitality are likely to be negatively affected under ongoing climate change on Marion Island if this brings about heavier epiphyte loads on this keystone cushion plant species.

Opsomming

In die afgelope eeu het die klimaat in die Antarktiese en sub-Antarktiese gebiede merkwaardige verandering getoon. Die Suidelike See Eilande dien as goeie modelle vir studies verwant aan die gevolge van klimaatsverandering, aangesien die kort termyn effekte in die gebiede duideliker mag wees in die toekoms. Marion Eiland is ‘n voorbeeld van so ‘n sisteem, met ‘n ruwe abiotiese omgewing en lae spesies rykheid, wat vatbaar is vir verandering. Daar word voorspel, en is reeds bevind dat klimaatsverandering biologiese gevolge op plant gemeenskappe het, in terme van morfologie, fenologie en die interaksie tussen individue en spesies. Hierdie studie ondersoek die assosiasie tussen die hoeksteen plant spesie, *Azorella selago* (Apiaceace), en sy dominante epifietiese gras, *Agrostis magellanica* Lam. (Poaceae). Die studie is op twee komplimentêre maniere benader, naamlik deur waarneming en eksperiment. Die hoof doel van die studie was om die biotiese belang van mikroklimaat temperatuur te kwantifiseer, en die hoeveelheid epifiete, die morfologie en die fenologie van *A. selago* te bepaal by drie verskillende hoogtes op Marion Eiland. Laasgenoemde het inligting verskaf oor die variasie in die reaksie van plante tot die eksperimentele aspek van die studie, waarteen patrone vanaf toekomstige biologiese beheer vergelyk kon word. Deur plante te bestudeer by verskillende hoogtes bo seespieël word ‘n moontlike analoog vir die gevolge van temperatuur-verwante klimaatverandering in terme van die ekologie van *A. selago*, en laasgenoemde se interaksie met *A. magellanica* verskaf. Die mikroklimaat temperatuur geassosieer met *A. selago* verskil tussen dié drie liggings. Die versil was verwant aan die plaaslike topografiese toestande en die verskillende hoogtes bo seespieël. Die grootte van die kussingplante het duidelik versil tussen die drie liggings, met die verskille verwant aan die omgewing se heterogeneïteit, byvoorbeeld die verskille in ouderdom en substraat struktuur. *Azorella selago* se jaarlikse groeitempo was bepaal deur die stingel lengte en die aantal blare, op beide die wat oorskadu is deur die gras, en die was nie oorskadu is nie. Daar is gevind dat die faktore wat bygedra het tot die jaarlikse groeitempo van *A. selago*, varieër binne die verskillende liggings, en bedekking deur epifiete. Dit beklemtoon die belang van spesifisiteit van ligging wanneer groeitempo in en tussen die liggings van verskillende hoogtes bepaal word. Die blaar eienskappe het verskil tussen

verskillende liggings, as gevolg van plaaslike habitat toestande, soos topografie en bedekking deur epifiete. Soos verwag, het die blare wat oorskadu was deur *A. magellanica* ‘n groter spesifieke blaar area getoon as blare wat blootgestel was. Die hoeveelheid en digtheid van *Agrosits magellanica* was verwant aan hoogte bo seespieël, met *A. selago* wat fasiliterende effekte toon op *A. magellanica.* Die tendens waargeneem in hierdie studie is dat ten spyte van die algemene fasiliterende effek van *A. selago* op *A. magellanica*, die abiotiese omgewingsdrempel op ‘n laer hoogte is vir *A. magellanica* as vir *A. selago*. Fenologiese verskille was ook duidelik tussen die drie liggings. Die doel van die eksperimentele deel van die studie was om die effek van die dominante epifiet, *A. magellanica*, te bepaal op bioties relevante mikroklimaat temperature, asook op die fenologie en fiesiese toestand van *A. selago*. Verskeie behandelings is aangewend op die kussingplante by die drie liggings om die effek van skaduwee van die epifietiese *A. magellanica* op die plante te bepaal, asook die effek van versteurings versoorsaak deur die behandelings. *Azorella selago* se mikroklimaat temperatuur het geen betekenisvolle verskille tussen behandelings getoon nie, wat voorstel dat epifitiese *A. magellanica* oor die algemeen geen effek op die kussingplante se mikroklimaat temperatuur het nie. Daar was ‘n negatiewe verwantskap tussen die hoeveelheid epifiete op *A. selago* en die persentasie blomme en blomknoppe op die kussingplante. Die plante se vitaliteit was ook afhanklik van epifiet bedekking, met ‘n hoër vitaliteit telling vir kussingplante bedek met lae gras as die bedek met hoë gras. Dit toon dat *A. magellanica* met *A. selago* wedywer, terwyl *A. selago* vir *A. magellanica* fasiliteer. Hoë epifiet getalle het negatiewe effekte op *A. selago* se vegetatiewe en reproproduktiewe nakoming, asook die kussingplante se vitaliteit. Die resultate van hierdie studie toon dus dat die vegetatiewe en reproduktiewe nakoming van *A. selago* en kussingplant vitaliteit heel moontlik negatief geaffekteer sal word indien klimaatsverandering op Marion Eiland hoër epifiet getalle op die sleutel kussingplant spesie tot gevolg sal hê.

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Contents

Chapter 1: General introduction

Marion Island

Marion Island (46º 55'S, 37º 45'E) is the larger of the two Islands that form the Prince Edward Islands group. The Islands have been part of South Africa for over 50 years, when they were annexed and declared nature reserves by the South African government in 1948 (van Zinderen Bakker Sr. 1971). South Africa maintained a permanent base station on the eastern side of the Island, in Transvaal cove where a meteorological station was set for observational purposes (Hanel and Chown, 1999). The science was relatively informal, however, activities at the station soon expanded when scientific work started over the 1965/66 summer, and has been consistent till to date (Hanel and Chown, 1999). Marion Island is situated 1800 km on the southeastern part of Africa, and 2300 km north of Antarctica (Smith and Steyn, 1982) (Figure 1). This Island is of volcanic origin, with an age estimate of approximately 250 000 years (Pakhomov and Froneman, 1999). It is estimated to be approximately 300 km^2 in area, with a steep, irregular topography, rising from sea level to 1230 m a.s.l. in less than 5 km (Huntely, 1970). The climate experienced on the Island is an exceptionally isothermally oceanic tundra climate, with mean temperatures of 6.4 °C, and an annual precipitation just over 2000 mm per year (le Roux and McGeoch, 2007). The dominant northwesterly winds can reach gale-force in more than 100 days a year (Smith and Steenkamp 1990), with a mean annual wind speed of 22.1 m/s (le Roux and McGeoch, 2007).

Azorella selago *as a keystone species*

Azorella selago Hook.f. (Apiaceae) covers the largest altitudinal range of vascular plants across Marion Island, occurring from sea-level to 765 m a.s.l. (Moore, 1968; Huntley, 1972; Gremmen, 1981; Orchard, 1989; Frenot et al., 1993; Smith et al., 2001). This cushion plant is widespread across the island (Huntley, 1972; Smith et al., 2001), and also dominant on fellfield habitat (Huntley, 1972). The fellfiled habitat is a mineral rich bare rock which

contains large amounts of volcanic ash and weathered lava particles (Smith and Steenkamp, 1990). *Azorella selago* occupies loose scoraceous slopes of volcanic rocks, recent lava flows and forelands of retreating glaciers (Huntley, 1970; Frenot et al., 1998), hence it is a pioneer species, which contributes to succession on the Island (Frenot et al., 1998). Furthermore, this plant species forms terraces on fellfield landscapes, also adding significantly to soil accumulation on these landscapes, thus forming a strong relationship with geomorphological processes (Selkirk, 1998; Boelhouwers et al., 2000; Brancaleoni et al., 2003). Finally, *A. selago* hosts a diversity of epiphyte species (i.e. moss, liverwort, lichen and vascular plant species) (Huntley, 1972; Brancaleoni et al., 2003; le Roux, 2004) and microarthropod species (i.e. Acari (mites) and Collembolla (springtails) species) (Barendse and Chown, 2001; Hugo et al., 2004). It is therefore regarded as a keystone plant species on Marion Island (sensu Begon et al., 1996). The Marion Island plant community growing epiphytically on *A. selago* includes as many as 17 non-vascular (the taxonomy of many remain incomplete), and at least another 16 vascular plant species (McGeoch et al. in press). Most of these species interact with *A. selago* through facultative epiphytic associations (le Roux, 2004) (Figure 2).

Epiphytes

Epiphytes generally represent about 10 % of the total vascular plant diversity on Earth, spending much or all of their lives attached to other plants (Hietz, 1998). However, they are non-parasitic since they do not derive nutrients or water directly from their host (Benzing, 1987; Nadkarni et al., 2001). Epiphyte plants require a suitable rooting medium, microclimate, and stable substrate; however, these conditions could be diverse and similar to those required by terrestrial vegetation (Benzing, 1987).

There are three categories of epiphytes, which include accidental, obligate, and facultative epiphytes (Benzing, 1987; Benzing, 1989; Nadkarni et al., 2001). Accidental epiphytes consist of plants that grow terrestrially though they occasionally grow on another plant substrate to reach maturity (Nadkarni et al., 2001). Obligate epiphytes depend entirely on their host for structural support, without deriving nutrients from their host (Nadkarni et al., 2001). Finally, facultative epiphytes include plants that usually grow both epiphytically

and terrestrially (Nadkarni et al., 2001). An example of a facultative epiphyte is *Agrostis magellanica* Lam. (Poaceae) on *A. selago* cushions on the sub-Antarctic Prince Edward Islands (Benzing, 1989). This grass species is the dominant epiphyte growing on *A. selago* cushions, even though it also grows in mires, in edges of ponds to the fellfield matrix, and in small numbers in all habitats at low altitudes from sea-level to 585 m a.s.l (Gremmen and Smith, 2004).

Associations between plants and epiphytes can vary between positive and negative, depending on how these responses vary in strength (Stone and Roberts, 1991; Miller, 1994; Berlow, 1999; Levine, 1999). Positive interactions arise from similar environmental requirements or as a result of some dependency or benefit to one or both of the species involved (John and Dale, 1995). Positive relationships are facilitative, where the substrate on which vegetation is growing is insulated, thus maintaining warmer temperatures, resulting in an increased boundary layer of the whole plant community (Choler et al., 2001). Negative interactions result from different environmental requirements or due to competition effects or other interactions that may prevent species co-existence (John and Dale, 1995). There are a number of factors influencing positive and negative associations in plant communities. For example, moisture conditions within the host plant, substrate microclimate, and nutrient availability affect the colonization and survival of epiphytes (Hietz and Briones, 1998; Choler et al., 2001; Zotz and Hietz, 2001; Callaway et al., 2002). Previous studies showed that positive and negative species associations between plants along gradients are influenced by environmental changes (Callaway and Walker, 1997; Choler et al., 2001; Cavieres et al., 2006).

Global climate change

Global average surface temperature has increased by approximately 0.74 °C over the last century (IPCC, 2007). This includes the updated 100 year trend from 1906 to 2005 (0.56 to 0.92) °C which is larger than the corresponding trend for 1901 to 2000 of 0.6 (0.4 to 0.8) °C last reported (IPCC, 2007). The Northern Hemisphere is likely to have had the largest temperature rise in the twentieth century, with 1998 experiencing the warmest temperatures

on record (IPCC, 2001; IPCC, 2007). However, there is not sufficient temperature data available for the Southern Hemisphere before the last 1000 years (IPCC, 2001). Previous studies report gradual climate changes at the Southern Hemisphere when compared to the Northern Hemisphere over the past 50 years (Kennedy, 1995; IPCC 2001). Global Circulation Models predict that climate change effects will be more prominent in the polar regions (Smith 1994; Beniston et al., 1997). The Antarctica is an example of such a region reported to be affected by climate change, with up to 1°C increases in surface air temperatures per decade (Smith 1994; Beniston et al., 1997). It is also predicted that variability in the distribution (temporal and spatial) patterns of precipitation will increase as a result of climate warming, although it is difficult to include precipitation in climate change models due to the fact that water exists in various forms (i.e. ice, snow, free water, and water vapor) (Hodkinson et al. 1999). Climate reports from the Antarctic and sub-Antarctic Islands show rapid environmental warming coupled with changes in precipitation patterns over the last 30 to 50 years (Walther et al., 2002).

A sub-Antarctic example: Climate change on Marion Island

The sub-Antarctic Marion Island is a high latitude system, suitable for studying climate change biotic implications. This Island experiences oceanic climates, with a mean temperature difference of 3.6 °C between the coldest and warmest months, and mean diurnal variation of 1.9 °C (Smith, 2002). Marion Island has experienced rapid climate change over the past 50 years when compared to the Northern Hemisphere (Kennedy, 1995; IPCC 2001). The coldest recorded month is August with an average temperature of 3°C, and February being the warmest, with an average temperature of 7°C (Huntely, 1972). The changes in climate on Marion Island include an increased temperature of the five hottest years between the 1950's and 1990's, from an average of 5.5 to 6.8 °C respectively (le Roux and McGeoch, 2007). Climate change also altered the mean daily maxima and minima temperatures, which increased from an average of 7.6 °C (1950's) to 8.6 °C (1990's) (le Roux and McGeoch, 2007). Annual rainfall decreased by 1.5 mm over the recorded period of 1960's and 1990's, with a decline on mean and maximum duration of consecutive days without rainfall (le Roux

and McGeoch, 2007). Previous studies also report an increase of sunshine by 3.3 hours per year, as well as an increase of 1.4 ºC in sea temperature (Smith, 2002; Mélice et al., 2003). Climate change is likely to directly and indirectly (e.g. via invasive species and changes in species interactions) affect the indigenous biota on Marion Island (Smith, 2002; le Roux et al., 2005; McGeoch et al., 2006). There is indeed evidence of significant effects of climate change on the biota of Marion Island (Smith, 2002; le Roux et al., 2005; McGeoch et al., 2006).

Predictions and current consequences of global climate change

Predictions for the biological consequences of ongoing climate change are already reported for Marion Island. For example, it has been predicted that plants will increase their altitudinal limits upslope on the island, as also affecting the primary productivity, nutrient cycling, vegetation and habitat structure (Smith and Steenkamp, 1990; Smith et al., 2001; le Roux et al., 2005). Further warming may also increase the pool of potential invasions by exotic species on this island, as well as the spread of already established exotics (Bergstom and Chown, 1999; Smith, 2002). This could potentially have serious consequences for community structure and functioning (Gremmen et al., 1998). The spread of the introduced house mouse, *Mus musculus* L. (Muridae) is also thought to be increased by recent warming on Marion Island (Smith, 2002), competing with the Lesser Sheathbills *Chionis minor* (Huyser et al., 2000). The house mouse also feeds on the indigenous species, *Uncinia compacta* R. Br. (Cyperacea) and ectemnorhinine weevil species (Chown and Smith, 1993). In addition, experimental manipulations of precipitation report greater *A. selago* cushion senescence, suggesting an interaction with wind patterns to result in a directional die back and degradation of cushions (le Roux, 2004; le Roux et al., 2005; McGeoch et al., 2006). Species interactions are also predicted to be highly sensitive to climate change, resulting in complex trophic interactions and community structures (Cramer, 1997; Convey, 2000; McGeoch et al., 2006).

Climate change effects on plant interactions

Interactions between species determine the success of species within a community and the success can be measured through the abundance, diversity, and stability of the entire community (Begon et al., 1996). In order to understand complex species relationships, the effects of various, often simultaneous species interactions in which a species is involved needs to be examined (Miller, 1994). Direct and indirect interactions both determine the net effect of one species in a community (Levine, 1976; Miller, 1994). An indirect effect refers to the effect of one species on another through direct effects on the resource consumption of one or more intermediate species (Levine, 1976; Schmitt, 1987; Miller, 1994). Direct interactions constitute the effect of a species on another through sharing the same, abiotic limiting resources (Miller, 1994). These interaction pathways are not only complex, but also predicted to result into more complex interactions and a complex range of responses to climate change (Cramer, 1997; Convey, 2000; McGeoch, 2007; Brooker et al. in press). Epiphytic communities in particular are generally expected to demonstrate drastic responses to ongoing climate change (Nadkarni and Solano, 2002).

Azorella selago and its dominant epiphyte, *A. magellanica* form an interaction that is predicted to be highly sensitive to climate change (le Roux et al. 2005; McGeoch et al. in press). *Agrostis magellanica* is a facultative epiphyte since it has low dependency on *A. selago* at low altitude areas (Benzing, 1989), although it is a dominant epiphyte colonizing the cushion plant across the island. A previous study on Marion Island reports a 6.4 % of each cushion's surface covered by epiphytic *A. magellanica* and also predicts that this grass might also be affected by further climate change (le Roux et al., 2005). *Agrostis magellanica* occurs from sea-level to approximately 550 m a.s.l. on Marion Island (le Roux, 2004). Warming alone could cause an increase in abundance of most epiphyte species (le Roux et al., 2005), which include moss, liverwort, lichen and vascular plant species (Huntley, 1972; Brancaleoni et al., 2003; le Roux, 2004); also expanding their altitudinal ranges upslope. This could bring about much heavier shading of *A. selago,* leading to a short-term increase in stem mortality under longer-term shading (le Roux et al., 2005). This dominant epiphyte, *A. magellanica* is distributed on Marion Island, Prince Edward Island, Crozet, Kerguelen, Macquarie, Antipodes, Auckland, Campbell, Tristan da Cunha, Gough, Falkland Islands,

South America, and New Zealand (Gremmen and Smith, 2004). In the sub-Antarctic Islands, *A. magellanica* also dominates mires, although it also grows in smaller numbers in all habitats as well as from the edges of ponds to the fellfield matrix (Gremmen and Smith, 2004). This grass species often inhabits *A. selago* cushions as a facultative epiphyte as mentioned above. *Azorella selago* cushions accumulate humus within its hemispherical structure, created through its ability to retain its senescenced leaves (Huntely, 1972). Hence *A. magellanica* may be exploiting this cushion plant for its humus richness as well as warmer microclimates and stable substrate for seedling establishment. However, the nature of the interaction between *A. selago* and *A. magellanica* has never been directly examined, and the impact of the grass on cushion plants remains poorly understood.

Thesis aims and objectives of each chapter

The main objective of this research was to investigate the nature of the interaction between the dominant epiphyte, *A. magellanica* and its host plant, *A. selago*. Chapter 2 deals with quantifying biotically relevant microclimatic temperatures, as well as the morphology, epiphyte load and phenology of *A. selago* in three altitude sites on Marion Island. As reported in previous studies, altitudinal gradients encompass changes in temperature, precipitation, solar radiation intensity, partial pressure of atmospheric gases and vapor pressure gradients often across relatively short distances (Bowman et al., 1999, Cavieres et al., 2000). This change in climatic variables across altitude undeniably affects the phenology, morphology, and the interaction between individuals and species (Fielding, et al., 1999; Fitter and Fitter, 2002; Sanz-Elorza, et al., 2003). Results reported in the first chapter provided information on baseline variation for understanding the manipulative, experimental effects reported in the third chapter, and against which future patterns arising from biological monitoring can be compared.

The effect of the dominant epiphyte, *A. magellanica* on biotically-relevant microclimatic temperatures, as well as on the phenology and physical condition of *A. selago* is examined in the third chapter. This gives an understanding about the nature of the

relationship between *A. selago* and its dominant epiphyte, *A. magellanica*, which has never been directly examined. Previous studies report that the microclimate, phenological and reproductive performance, as well as the morphology of plants growing under sheltered environments is altered (Huntley, 1972; Frenot et al., 1993; le Roux et al., 2005). The three study sites were chosen at different altitudes in fellfield habitat to encompass an altitudinal range in understanding the variability in *A. selago* characteristics and those of its dominant epiphyte. Studying plants at different altitudes provides a possible analogue for the temperature-related climate change consequences for the ecology of *A. selago*, and its interaction with *A. magellanica*.

Finally, a general conclusion (Chapter 4) provides a brief summary and integrated overview on the main findings of the research from chapters 2, and 3 and also predicts climate change implications on the interaction between *A. selago* and *A. magellanica*. Each chapter is written as an individual manuscript and there is therefore some repetition of methods, species and site descriptions.

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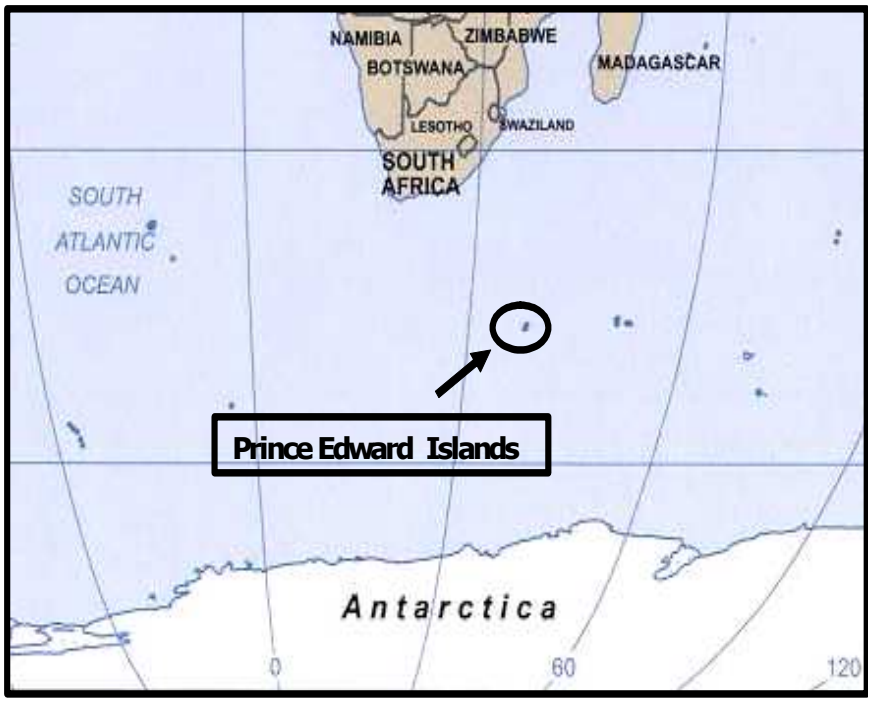
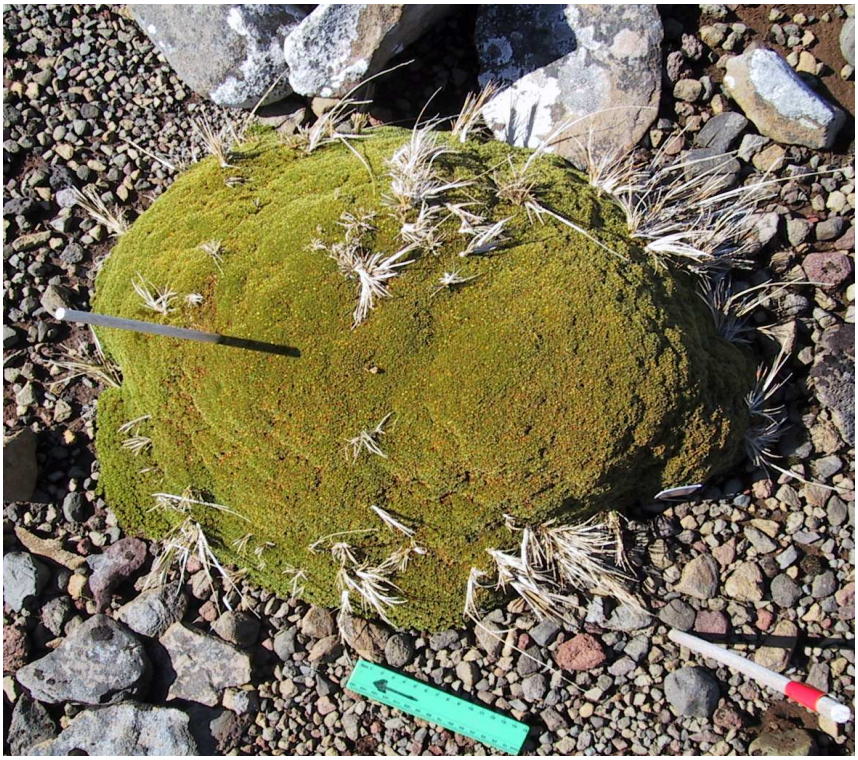


FIGURE 1. The location of Prince Edward Islands in the Southern Ocean.



FUGURE 2. Azorella selago *on a fellfield matrix with its dominant epiphyte,* Agrostis. magellanica*, growing on it. The ruler represents the scale (15 cm) as well as direction (arrow pointed to the north).*

Chapter 2: Patterns of *Azorella selago* cushion size and morphology, epiphyte load and phenology at three altitudes on Marion Island

Introduction

Plant species that cover a broad range of altitudes and latitudes are useful in examining biotic responses to changes in altitude, associated with climate change (Andrew et al. 2003). Altitudinal gradients encompass changes in temperature, precipitation, intensity in solar radiation, partial pressure of atmospheric gases and vapor pressure gradients often across relatively short distances (Bowman et al., 1999, Cavieres et al., 2000). This change in climatic variables across altitude undeniably affects the phenology, morphology, and the interaction between individuals and species (Fielding, et al., 1999; Fitter and Fitter, 2002; Sanz-Elorza, et al., 2003). Therefore, climate change is likely to cause shifts in species distributions and physiologies, resulting in elevation shifts or changes in species morphology and phenology (Walther et al. 2002; Penuelas and Boada, 2003; Root et al., 2003). This has indeed been shown in species ranging from birds, amphibians, insects and plants, for example, phenological or behavioural events have shifted earlier by comparison with the previous four decades (Fitter and Fitter, 2002; Root et al., 2003; Walther, 2003).

Species ranges are a result of basic habitat requirements, which satisfy, for example, their metabolic temperature tolerance, thus determining current distribution (Saetersdal et al., 1998; Root et al., 2003; Parmesan et al., 2005). Studying these altitudinal gradients offers an analog for future climates (Hodkinson and Bird, 1998; Hodkinson and Wookey, 1999). For example, studying the distribution pattern of a species at warmer, lower altitudes serves as an analog for the potential response of plants currently at cooler high altitude areas to increased temperature. Similarly, the analog can be applied to a cooling scenario, where high altitudes are regarded as a predictor of changes that may be observed at low altitudes (Tweedie and Bergstrom, 2000). This approach has been previously applied in other studies, where an increase in leaf production and reproduction output was predicted for six plant species on sub-Antarctic Macquarie Island under climate warming (Tweedie, 2000). Smith et al. (2002) also used elevation as an analog of climate change to analyze climatic influence on soil properties

on sub-Antarctic Marion Island, where this in turn affected the abundance of plant communities and caused ecosystem desertification.

However, conclusions reached from altitudinal gradient studies need to be made cautiously as they are only a distal predictor of the determinants of plant characteristics and distribution patterns (Austin et al., 1984). In order to understand plant patterns along an environmental gradient, it is important to use variables that are related physiologically to the growth of plants (Pausas and Austin, 2001). Thus, experimental studies are often implemented to compliment gradient studies and to control the effect of other environmental factors while studying a single or few target variables to predict the impact of climate change on species characteristics and distributions (Dunne et al., 2004; Parmesan et al., 2005). For example, temperature may be increased without changing humidity and sunlight. Nonetheless, these experimental approaches generally provide insight on short-term effects relative to field based species distribution and patterns which represent long-term responses to gradual climate change (Rustad et al., 2001).

High latitude ecosystems provide good models for altitudinal studies related to climate change effects, since effects may be evident in the short term and may also be clearer (Davies and Melbourne, 1999). In the southern hemisphere, the Antarctic and sub-Antarcic Islands experience double the global average change (Smith and Steenkamp, 1990). Furthermore, these ecosystems are remote, closed systems, with harsh environments accommodating low species richness which are often vulnerable to change (Smith and Steenkamp, 1990; Callaghan et al., 1992; Davies and Melbourne, 1999). Marion Island in the sub-Antarctic is one island where climate change is very pronounced (Kennedy, 1995; IPCC 2001).

Marion Island is situated 1770 km south of South Africa and is part of the Prince Edward Island group (Hänel and Chown, 1998). The island has experienced gradual climate change over the past 50 year when compared to the northern hemisphere (Kennedy, 1995; IPCC 2001). The changes in climate on Marion Island include an increased temperature of the five hottest years between the 1950's and 1990's, from an average of 5.5 to 6.8 °C respectively (le Roux and McGeoch, 2007). Climate change also altered the mean daily maxima and minima temperatures, which increased from an average of 7.6 °C (1950's) to 8.6 °C (1990's) (le Roux and McGeoch, 2007). Annual rainfall decreased by 1.5 mm over the recorded period of 1960's and 1990's, with a

decline on mean and maximum duration of consecutive days without rainfall (le Roux and McGeoch, 2007). Previous studies also report an increase of sunshine by 3.3 hours per year, as well as an increase of 1.4 ºC in sea temperature (Smith, 2002; Mélice et al., 2003). Climate change is likely to directly and indirectly (e.g. via invasive species) affect the indigenous biota on Marion Island (Smith, 2002; le Roux, et al., 2005; McGeoch, et al. in press). It is predicted that the upper altitude margins of vascular plant species ranges on the island may change. There is indeed evidence of significant effects of climate change on the biota of Marion Island (Smith, 2002; le Roux, et al., 2005; McGeoch, et al., 2006).

Another indirect threat on the biota and ecology of this Island is the further invasion of invasive species (Smith, 2002). Warmer climate will favour exotics because they often spread more rapidly with an increase in temperature (Smith, 2002; Frenot et al., 2005). Previous studies reported expansions of invasive mosses, grasses, and other vascular plants over the last decade (Gremmen et al., 1998; Gremmen and Smith, 1999). However, on Marion Island there have only been predictions of possible plant altitudinal shifts with no significant evidence. This Island supports diverse plant biota occurring over a broad range of habitats and over large altitudinal limits (Smith and Steenkamp, 1990).

Azorella selago Hook.f. (Apiaceae) covers the largest altitudinal range of vascular plants across Marion Island (Huntley, 1970). An experiment simulating current climate change trends was recently conducted on Marion Island to study the effects of reduced rainfall and increased temperature on *A. selago* (le Roux, et al., 2005). Continued warming and drying of the island will potentially cause this cushion plant to move to higher altitudes, although also shortening its growing season and causing increased rates of dieback (le Roux et al., 2005). The dominant epiphyte on *A. selago*, *Agrostis magellanica* Lam. (Poaceae) might also be affected. Warming alone could cause an increase in abundance of most epiphyte species (le Roux et al., 2005), also expanding their altitudinal ranges upslope. Epiphyte species on Marion Island include moss, liverwort, lichen and vascular plant species (le Roux, 2004). The predicted consequences of climate change would bring about much heavier shading on *A. selago*, leading to a short-term increase in stem mortality under longer-term shading (le Roux et al., 2005). However, the nature of the interaction between *A. selago* and *A. magellanica* has never

been directly examined, and the impact of the grass on cushions plants remains poorly understood.

The objectives of this study were to quantify biotically-relevant microclimatic temperature, as well as the morphology, epiphyte load, and phenology of *A. selago* in three sites on Marion Island. This will provide information on baseline variation for understanding the manipulative, experimental effects reported in the next chapter, and against which future patterns arising from biological monitoring can be compared. The impact of the dominant epiphyte on *A. selago* is then examined in the following chapter. The three study sites were chosen at different altitudes in fellfield habitat to encompass altitudinal range in understanding the variability in *A. selago* characteristics and those of its dominant epiphyte. Studying plants at different altitudes provides a possible analogue for the temperature-related climate change consequences for the ecology of *A. selago*, and its interaction with *A. magellanica*. Temperatures at higher altitudes are relatively colder, and ongoing climate change is predicted to cause an upward shift in the distribution of vascular plant species on Marion Island. Climate change may also affect the interaction between *A. selago* and *A. magellanica*, which has never been directly examined on Marion Island.

Materials and methods

SPECIES DESCRIPTION AND HABITAT

Azorella selago is a cushion forming herbaceous dominant plant species occurring from sea-level to 765 m a.s.l. on Marion Island (Huntley, 1970; Frenot et al. 1993). It is widely distributed on the Macquarie, Crozet, Kerguelen, Heard, and Prince Edward Islands in the sub-Antarctic, where it plays a significant role in the vegetation of these islands (Huntley, 1972). Its tolerance to cold, harsh, and exposed environments is mainly attributed to its hard compact growth form. Water and heat loss are reduced through its tightly packed leaves and stems growing closely to each other (Huntley, 1972; Callaghan and Emanuelsson, 1985; Orchard, 1989).

Azorella selago is widespread across the island (Huntley, 1972, Smith et al., 2001), and also dominant in fellfield habitat (Huntely, 1972; Orchard, 1989; Frenot et al., 1993). The fact that this cushion occurs from sea-level to 765 m a.s.l. on Marion Island (Huntlely, 1970; Frenot et al., 1993) makes it the vascular plant species with the largest altitudinal range on the island (Moore, 1968; Gremmen, 1981; Smith et al., 2001). *Azorella selago* occupies loose scoraceous slopes of volcanic rocks, recent lava flows and forelands of retreating glaciers (Huntley, 1970; Frenot et al., 1998), hence it is a pioneer species which contributes to succession on the Island (Frenot et al., 1998). Furthermore, this plant species forms terraces on fellfield landscapes, also adding significantly to soil accumulation on these landscapes, thus forming a strong relationship with these geomorphological processes (Selkirk, 1998; Boelhouwers et al., 2000a; Brancaleoni et al., 2003). Finally, *A. selago* hosts a diversity of epiphyte species (i.e. moss, liverwort, lichen and vascular plant species) (Huntley, 1972; Brancaleoni et al., 2003; le Roux, 2004) and microarthropod communities (i.e. Acari (mites) and Collembolla (springtails) species) (Barendse and Chown, 2001; Hugo et al., 2004). It is therefore regarded as a keystone plant species on Marion Island (sensu Begon et al., 1996). The Marion Island plant community growing epiphytically on *A. selago* includes as many as 17 non-vascular (the taxonomy of many remain incomplete), and at least another 16 vascular plant species (McGeoch et al. in press). Most of these species are facultatively epiphytic at low altitudes (le Roux, 2004). However, the grass, *Agrostis magellanica* is the dominant epiphyte growing on *A. selago* cushions (Huntley, 1972; Gremmen, 1981; le Roux, 2004).

Fellfield habitat is characterized by nutrient-poor, mineral soils with high rock cover (Smith et al., 2001; Gremmen and Smith, 2004). It forms in higher altitude areas strongly exposed to wind and low temperatures compared to lower-lying areas (Gremmen, 1981). This habitat is regarded to be the oldest of the habitats on the sub-Antarctic islands (Scott, 1985). As mentioned above, *A. selago* is the most dominant plant species in various plant communities, but is most well developed on fellfield habitats occurring in almost monoculture-like stands (with the exception of its epiphytes, bryophytes and other non-vascular species) (Frenot et al., 1993).

SAMPLING

Azorella selago was sampled in grey lava, mesic fellfield habitat on Marion Island (Figure 1: Chapter 1). The study was conducted from April 2004 to April 2005 in the three study sites on the eastern side of the island, i.e. Skua Ridge, Tafelkop and Tafelberg (Table1). Sites within altitude were not replicated in this study because the primary objective was first to quantify baseline variation on the relationship between *A. selago* and its dominant epiphyte, and then to test the relationship (next chapter) in three different areas to gain some understanding of location specific variability in plant responses to treatments (see Chapter 3).

Ten, randomly selected low-density, and 10 high-density *A. magellanica* covered *A. selago* cushion plants were selected for observations at each site. Plants free of mouse burrows dug by the alien invasive mouse species *Mus musculus* L. (Muridea) (Chown and Smith, 1993) were selected. Plants of moderate size were chosen (circumference ranged from 37 to 477 cm amongst all sites) to avoid extreme size effects. Every effort was made not to damage small plants because of the low recruitment rates of the species (le Roux and McGeoch, 2004). Small *A. selago* plants do not have significant *A. magellanica* numbers relative to moderate sized plants, and larger plants tend to have more dead tissue due to aging and heavy epiphyte covers. A study conducted by Alliende and Hoffman, (1985) on another cushion plant *Laretia acaulis* (also Apiaceae) suggested that larger cushions have more possibilities of being colonised by more epiphytes. To control for some of this unwanted variability, plants in the extreme size categories were excluded in this study. Plants within the selected size range (37 – 477 cm circumference) were randomly selected and were at least three plants apart from each other to avoid pseudo-replication. Plants may be considered independent of each other because of the consistent absence of, or extremely weak, spatial autocorrelation in plant characteristics across patches (Hugo, 2006; Nyakatya, 2006).

The selected plants were marked with aluminium tags and short wooden marker poles. Position was determined using a Garmin 12MAP GPS (Garmin International, Kansan City, USA). All plants were photographed with a digital camera (photograph taken from approximately 1.5 m above each plant), with a scale and compass direction

marker included in each photograph. This was done to calibrate the size and orientation of the plants.

MICROCLIMATE

The temperature within *A. selago* cushions was measured by i-button (Thermochron DS19221G, Dallas Semi-Conductors, Texas, USA) data loggers for a period of 11 months for the Skua Ridge (low site) and Tafelkop (mid site), and 10 months for Tafelberg (high site). I-buttons were set to measure temperature (°C) at two hour intervals, then inserted 1-2 cm into the cushion with a tag sticking up out of the cushion. Insertion was performed on 5 of the cushions selected with low *A. magellanica* density, and 5 of the selected cushions densely covered with *A. magellanica*. Insertion took place in May, followed by removal in September 2004 to download temperature measurements. I-buttons were reinserted into the same cushions in October 2004 and removed in March 2005.

CUSHION SIZE

Azorella selago size measurements that were taken included maximum and perpendicular diameter, circumference, and height. Plant circumference was measured by running a tape measure around the cushion plant. Height was determined by measuring the vertical distance between the highest and lowest point of the plant surface and the ground beneath it. The average of the two height measurements was calculated. All measurements were taken in cm.

LEAF MORPHOLOGY

Determining leaf morphology involved sampling *A. selago* cushions with high-density *A. magellanica* from the three sites (low = 8, mid = 5, high = 8 cushions). Five *A. selago* stems growing in-between *A. magellanica* stems and five from the exposed area of the

same plant (plant surface area not covered with *A. magellanica*) were picked. Sampling was limited to five stems per plant to minimize damage to the plant. The length of the stems and number of leaves were used to calculate cushion stem growth rate. Stem length was determined by measuring the length of the green part on each leaf in cm. Leaves from each stem were separated to count the number of green leaves per stem, after which the third green leaf from the bottom of every stem was selected. The third green leaf from the bottom was selected from all stem samples to standardize the sampling method at all three altitude sites. This leaf was weighed with a microbalance (Metteler AE163) to five decimal places in grams, and its trichomes counted from the ventral surface, where trichomes occur. All weighed leaves were permanently pressed to a white cardboard with transparent tape from which leaf images were captured using a flatbed scanner (HP Scanjet 5470c). Trichome density and specific leaf area were determined by image analysis of the pressed leaves (SigmaScan Pro version 5).

EPIPHYTE LOAD AND CUSHION VITALITY

A separate observational component of the study was performed to quantify *A. magellanica* load, percentage surface area with grass and cushion vitality of *A. selago* cushions at the same three sites. This could not be quantified from the 20 previously chosen cushions per site (see sampling) because the latter were specifically chosen on a basis of having low and high grass density. Therefore, 100 cushions were randomly selected within each of the three sites and the number of epiphytic *A. magellanica* clumps was counted on each cushion. Clump size was not considered when determining *A. magellanica* number. *Agrostis magellanica* growing off *A. selago* cushions in the grey lava matrix was also counted by walking 10 x 20m transects and counting the number of grass clumps. The percentage cushion surface area covered by *A. magellanica* was estimated by qualitative rating of epiphyte cover on a scale of 0 – 100% (0 = no grass, 100 = cushion surface completely covered by grass). Cushion vitality was also determined by rating each cushion at a scale of 1 – 10 (1-3 = very weak, 4-6 = clearly reduced but still healthy, 7-8 = normal, 9-10 = healthy plant with no sign of die-back or decay) (following Huntley, 1972).

PHENOLOGY

Phenological variables were measured for *A. selago* every month. At the low and middle altitude sites, phenology was monitored from August 2004 to February 2005, and at the highest altitude from October 2004 to February 2005. Weather conditions at high altitudes were relatively colder with cushions still covered with some snow, as a result of which measuring phenological variables only commenced in October.

Analysis

To test for the effect of site (i.e. the three sites at different altitudes) on cushion size variables, an Analysis of Variance (ANOVA) (Stat Soft, Inc. 1984-2003) was used. The difference in leaf morphology between altitude sites was tested using different tests. A Nonparametric, Kruskal-Wallis Analysis of Variance (Stat Soft, Inc. 1984-2003) was used for number of leaves on exposed and shaded stems, as well as for shaded number of trichomes. However, an Analysis of Variance (ANOVA) (Stat Soft, Inc. 1984-2003) was used to test for the difference between altitude site for the rest of the morphological variables. Log_{10} transformations were used to achieve normal distributions for exposed leaf mass, exposed and shaded leaf area, and exposed and shaded specific leaf area. An Analysis of Variance (ANOVA) (Stat Soft, Inc. 1984-2003) was used to test for the effect of epiphytic *A. magellanica* on *A. selago* stem and leaf characteristics. Log_{10} transformations were used to achieve normal distributions for stem length, leaf number, leaf mass, leaf area, specific leaf area and trichome number. To test for the effect of altitude site on epiphytic *A. magellanica* number and density, an Analysis of Variance (ANOVA) (Stat Soft, Inc. 1984-2003) was used. The effect of altitude site on the number of *A. magellanica* off cushions was tested using an Analysis of Variance (ANOVA) (Stat Soft, Inc. 1984-2003). Epiphyte number and density data was also log_{10} transformed to achieve normal distributions. The effect of altitude site on *A. selago* vitality was tested using a Nonparametric, Kruskal-Wallis Analysis of Variance (Stat Soft, Inc. 1984-2003). All these results are presented as either tables or box plots.

Results

MICROCLIMATE

The temperature associated with *A. selago* at the three sites on the island was, on average, between 4.83 and 5.86 °C higher in summer than winter (low altitude site difference = 5.12 °C, mid = 4.83 °C, high = 5.86 °C) (Figure 1, Appendix A). The low altitude site temperature in winter was on average 0.25 °C cooler than the mid altitude and 1.7 °C warmer than the high altitude site, and the mid altitude 2.02 °C warmer than high altitude site (Figure 1, Appendix A). However, summer average temperature differences increased with altitude (low-mid altitudes = 0.04 °C, low-high = 1.03 °C, mid–high = 0.99 °C) (Figure 1, Appendix A). The low altitude site temperature declined by 1.62 °C from June to July, and increased from September to December by 4.33 °C (Figure 1, Appendix A). The mid altitude site temperature decreased by 0.93 °C from June to July, and increased by 5.57 °C from September until December. The high altitude site temperature decreased by 2 °C from June till July, and increased by 6.44 °C from September until December (Figure 1, Appendix A). The high altitude site had cooler temperatures, compared to both mid and low altitude sites (Figure 1, Appendix A). However, in winter, the mid altitude site was on average warmer than the low altitude site, compared to the summer season where temperature increased with increasing elevation (Figure 1, Appendix A).

CUSHION SIZE

There was a significant difference in *A. selago* maximum diameter between sites ($F_{2, 57}$ = 17.51, $p < 0.001$) (Table 2). The maximum diameters of cushions were larger in the high than in the low altitude site (on average high altitude site = 94.86 cm, low altitude site = 60.20 cm) (Table 2). On the other hand cushion perpendicular diameter was not significantly different between altitude sites ($F_{2, 57}$ = 2.38, $p = 0.10$) (Table 2). Cushion circumference differed significantly between altitude sites ($F_{2.57}$ = 22.17, $p < 0.001$) (Table 2). Circumference was strongly related to altitude site, with significantly larger

cushions at high than in the mid and low altitude sites (on average high altitude site = 54.77 cm, mid = 206.95 cm, low = 199.45 cm) (Table 2). Plant height also varied significantly between sites ($F_{2, 57} = 3.38$, $p < 0.05$) (Table 2). Low altitude *A. selago* plants were significantly higher than the mid altitude site plants, whereas the height of high altitude cushions was intermediate (on average low altitude site = 15.29 cm, mid = 13.51 cm, high = 12.43 cm) (Table 2).

LEAF MORPHOLOGY

The length of exposed *A. selago* stems differed significantly between altitude sites ($F_{2, 102} = 14.6$, $p < 0.001$) (Table 2). The low and high sites had longer stems than the mid altitude site (Table 2). Stems under shaded *A. selago* cushions also significantly differed between altitude sites ($F_{2, 102} = 4.7$, $p < 0.05$) (Table 2). The low area had longer stems than the mid altitude site (Table 2). The number of green leaves on exposed *A. selago* stems differed significantly between sites ($H_2 = 9.44$, $N = 105$, $p < 0.001$) (Figure 2a). Exposed stems had the most green leaves at the low altitude relative to the mid altitude site, whereas the number of leaves was intermediate in the high altitude site (Figure 2a). However, the number of leaves on shaded stems did not significantly differ between sites ($H_2 = 0.44$, $N = 105$, $p = 0.79$) (Figure 2b). There was a significant difference in exposed leaf mass between sites ($F_{2, 102} = 22.64$, $p < 0.001$) (Table 2). The high altitude had significantly heavier leaves relative to the mid altitude site, and the mid site had bigger leaves than low altitude site (Table 2). There was a significant difference in shaded leaf mass between altitude sites ($F_{2, 10} = 13.18$, $p < 1.10$) (Table 2). The high altitude had significantly heavier leaves than the mid altitude site, and heavy low altitude leaves relative to mid altitude site (Table 2).

There was also a significant difference in exposed leaf area between sites ($F_{2, 102} = 8.16$, $p < 0.01$) (Table 2). Low altitude exposed leaf area was significantly bigger than the mid site exposed leaf area, and high altitude exposed leaf area significantly bigger from the mid altitude site exposed leaf area (Table 2). Shaded leaf area also differed significantly between sites ($F_{2, 102} = 12.66$, $p < 0.01$) (Table 2). High altitude shaded leaves were significantly bigger than both low and mid altitude site leaves (Table 2).

There was significant difference in exposed specific leaf area between altitude sites (H_2 = 19.08, N = 105, $p < 0.01$) (Table 2). The mid altitude had significantly bigger leaves than both low and mid altitude sites (Table 2). Shaded specific area also differed significantly between sites ($F_{2, 102}$ = 14.38, $p < 0.01$) (Table 2). The mid altitude had significantly bigger leaves than the low altitude site, whereas the specific leaf area of high altitude site cushions was intermediate (Table 2).

The number of trichomes on exposed leaves strongly and consistently decreased with increasing altitude, with significantly more trichomes at the low altitude site than mid and high altitude sites ($F_{2,102}$ = 9.06, $p < 0.01$) (Table 2). Similarly, the lowest altitude site had significantly more shaded trichomes relative to both mid and high altitude sites (H_2 = 14.57, N = 105, $p < 0.01$) (Table 2). There was a significance difference in exposed trichome density between sites ($F_{2, 102}$ = 5.54, $p < 0.01$) (Table 2). High altitude exposed trichome density was significantly smaller than the low altitude site trichome density (Table 2). Shaded trichome density similarly showed a significant difference with altitude site, with a smaller trichome density at the higher altitude than at the low altitude site ($F_{2, 102}$ = 7.66, $p < 0.01$) (Table 2).

COMPARISON OF STEM AND LEAF CHARACTERISTICS BETWEEN EXPOSED AND SHADED CUSHION AREA

There was a significant difference in stem length between exposed and shaded cushion surface area ($F_{1, 206}$ = 23, $p < 0.001$) (Table 3). Exposed cushion surface area had longer stems than stems on shaded area (Table 4). There was no significant difference in the number of leaves between exposed and shaded stems ($F_{1, 206}$ = 2.67, $p = 0.1$) (Table 3). There was a significant difference in leaf mass between leaves from the exposed and under shaded cushion surface area ($F_{1, 206}$ = 16.36, $p < 0.001$) (Table 3). The exposed cushion surface area produced heavier leaves than the shaded area (Table 4). Leaf area also showed a significant difference between exposed and shaded leaves ($F_{1, 206}$ = 9.24, $p < 0.05$) (Table 3). Exposed leaves had a larger leaf area than the leaves on the shaded cushion surface area (Table 4). There was a significant difference in specific leaf area between exposed and shaded leaves ($F_{1, 206}$ = 4.82, $p < 0.05$) (Table 3). The shaded

cushion surface area produced bigger leaves than the exposed area (Table 4). Trichome number showed no significant difference between leaves picked on exposed and under shaded cushion surface area ($F_{1, 206} = 0.59$, $p = 0.44$) (Table 3). However, trichome density showed a significant difference between leaves on exposed and under shaded cushion surface area ($F_{1, 206} = 6.04$, $p < 0.05$) (Table 3). Leaves under shaded cushion surface area produced cushions with a higher trichome density than the exposed cushion area (Table 4).

EPIPHYTE LOAD AND VITALITY

There was a significant difference in epiphyte number between sites ($F_{2, 285} = 11.69$, $p < 0.001$) (Table 5). The low and mid altitude sites had significantly higher epiphyte density than the high site (Table 5). The same trend was observed also for *A. magellanica* density ($F_{2, 258} = 40.18$, $p < 0.001$) (Table 5, Figure 2d). The percentage surface area of cushions covered with *A. magellanica* decreased with increasing altitude, confirming the trend shown by *A. magellanica* number and density (Table 5). *Agrostis magellanica* growing off *A. selago* cushions was significantly different between sites ($F_{2, 27} = 21.09$, $p < 0.001$) (Table 5). All sites were different from each other; with the highest number of *A. magellanica* clumps at the low altitude site, intermediate at the mid altitude site, and least number of clumps at the high altitude site (Table 5). Cushion percentage surface area covered by *A. magellanica* was high at the low altitude site, where there was a highest range of percentage grass cover (Table 5). There was no significant difference in cushion vitality between sites ($H_2 = 1.63$, $N = 300$, $p = 0.44$) (Table 5, Figure 4). However, high altitude site cushions had a high vitality score when compared to both mid and low altitude site (Table 5, Figure 4).

PHENOLOGY

The percentage of green plant surface area on *A. selago* cushions was highest at the low altitude site for most of the months recorded (Figure 5a). From spring to summer, *A.*

selago green percentage cover increased for all altitude sites, by between 10 and 40% (low = 40%, mid = 15%, high = 10%) (Figure 5a). During the same period, percentage brown surface area decreased by approximately 50% at the low altitude, 30% at mid, and 20% at the high altitude site (Figure 5b). Flower buds emerged only in November and December, where the percentage surface area of flower buds increased by approximately 3% at the low altitude, 5% at mid and by 10% at the high altitude site over the two months (Figure 6). Flower buds later matured in January for all site (Figure 6). However, the flowering period at the low altitude site ended in February, whereas flowering continued into March at the mid and low altitude sites (Figure 6). Mid altitude site percentage flowering cover decreased by approximately 5%, and at the high altitude site this decreased by approximately 12% between February and March (Figure 6). The length of flower budding and flowering period was therefore shorter at the low altitude site, compared to mid and high altitude site. However, the first flower budding date was November for all three sites. Also, the percentage of the surface area cushion covered by flowers was greatest at the high altitude site than mid and low altitude site.

In October, the high altitude site had the most plants covered with green surface area than either mid and low altitude sites (Figure 7a). However, the low altitude site had the most plants with the highest percentage of green plant surface area (Figure 7a). A similar pattern was also observed in December and February (Figure 7b, c). In October the low altitude site had fewer plants covered with percentage of brown surface area than both mid and high altitude sites (Figure 7d). A different trend was observed in December and February, where low altitude sites had the most number of plants covered with percentage of brown surface area than mid and high altitude sites (Figure 7e, f). In November and December, the high altitude site had the most plants with low percentage cover of flower buds when compared to mid and low altitudes sites (Figure 7g, h). Nevertheless, the mid altitude site had the most plants with a high percentage of plant cover of flower buds than high and mid altitude sites (Figure 7g, h). In January, the low altitude site had the most plants with a low percentage of flowering plant surface area (Figure 7i). However, the high altitude site had the most plants with a high percentage plant surface area of flowers than mid and low altitude sites (Figure 7i). In February, there were more plants with a low percentage surface area of flowers at the high altitude site, when compared to mid and low altitude sites (Figure 7j). At the mid altitude site,

more plants had a high percentage surface area of flowers than high and low altitude sites (Figure 7j). The high altitude site had more green cushions compared to mid and low altitude sites, although the percentage cover of green cushions was highest at the low altitude site. Green percentage cover of cushions increased from August and peaked more in October and March at all three altitude sites. The percentage surface area of brown also decreased from August, and was at its lowest in January.

Discussion

There were apparent differences between the three study sites, as would be expected because of their positions at different altitudes. As expected the lowest site was on average warmer and the highest area colder. The temperature at the mid site at intermediate altitude was however very similar to the temperature at low altitude site. There was a 73 m difference between low and mid altitude sites, and a 199 m difference in altitude between the mid and high altitude sites. It is thus not surprising that the two lower sites were more similar in temperature. Nonetheless, not only altitude affects microclimatic temperatures. Local topographic conditions such as exposure and slope also play a role (Bonan, 2002). The low altitude site is exposed, with a moderate sloped topography, and the high altitude site also exposed with a gentle slope. However, the mid altitude site has gentle sloped topography, sheltered by hills on both the westerly and northern regions of the study site, thus providing a sheltered landscape that may result in warmer microclimate temperatures for these mid altitude site cushions.

There was a clear difference in cushion size between the three sites, with largest circumference on cushions at the high altitude site and smallest at the low altitude site. Cushions were however tallest at low altitudes. Low stature plants have an advantage of growing closer to the ground; therefore keeping plant leaves within the surface boundary layer thereby reducing low heat and water loss (Grace, 1977). Previous studies of cushion plants show similar results, accounting this cushions size difference to environmental heterogeneity such as differences in age and substrate structure (Pyšek and Liška, 1991; le Roux, 2004). High altitudes also have relatively uneven grey lava compared to the older grey lava at the low altitude sites. In this study, cushion growth at the high altitude

site is exposed to more obstructions than at the low altitudes where taller, low altitude cushions have an advantage of being able to grow over obstacles, maintaining their hemispherical shape than cushions growing at the high altitude sites (Verwoed, 1971; le Roux, 2004). Larger cushions have a higher chance of being exposed to unfavorable conditions (e. g harsh wind conditions, more colonization by other species). *Azorella selago* size on this study therefore appears to respond to environmental heterogeneity.

Cushion vitality did not markedly differ between the three study sites, confirming that *A. selago* thrives across a broad altitudinal range on Marion Island. Previous studies on the sub-Antarctic also report a broad altitudinal range for the cushion plant, *A. selago* (Huntley, 1972; Gremmen, 1981; Smith et al., 2002; McGeoch et al., 2006). There were 6.5 ± 2.5 green leaves on both shaded and exposed stems (Table 2). These results provide an estimate of annual growth for *A. selago*. This method is reliable and has been used elsewhere. For example, in a previous study on Kerguelen Island, the growth rate of *A. selago* cushions was determined with a one-off measurement at the end of the growing season as was the case in this study (Frenot et al., 1993). The current study shows that plants grew by producing six leaves over the growth period October/November 2004 to March/April 2005. Growth rate was however higher on exposed (non-shaded) stems in the low altitude site, with an average of seven leaves per stem. This may be attributed to the fact that *A. selago* growth rate shows a high within-site variability, with no apparent spatial structure associated with altitude (le Roux and McGeoch, 2004; Nyakatya, 2006). This highlights the importance of site-specificity when estimating growth rate within and between different altitude sites (le Roux and McGeoch, 2004). Site-specificity arises from environmental heterogeneity, such as the variability in soil type and moisture, nutrient availability, sunlight availability, aspect and microtopography (Bullock and Burkhart, 2005). In this study, the exposed stems at the low altitude site produced more green leaves, possibly showing high growth rates due to warmer temperatures and more exposure to solar radiation (Blake, 1996).

Leaf characteristics were different between the study sites with a smaller leaf area and lighter leaves at the mid altitude site than the low and high altitude sites. However, mid altitude cushions surprisingly produced leaves with larger specific leaf areas than the other two altitude sites. Leaf area is expected to be positively correlated to specific leaf area and leaf mass (Lambers et al, 1998). However, leaf size may be affected by diverse

environmental factors, such as temperature, rainfall and soil moisture, wind, frost frequency, nitrogen limitation and shading (Cavelier, 1996, Halloy and Mark, 1996, Schoettle and Rochelle, 2000; Tweedie, 2000). Previous studies have shown no significant evidence on how all these factors affect leaf size (le Roux, 2004). One possible reason for the smaller leaf area at the mid altitude site on this study could result from the relatively low wind frequency at the mid altitude, compared to the windier high altitude site. Leaf size and leaf boundary layer resistance increases with wind speed, hence smaller leaves have a relatively thin boundary layer resulting in efficient heat transfer, whereas larger, thinner leaves provide a thick boundary layer with inefficiency in heat transfer away from the leaf (Bonan, 2002). Therefore, larger, thinner leaves at the high altitude site in this study could serve as a defense mechanism by the plant in the windier high altitude site on Marion Island. The larger *A. selago* specific leaf area at the mid altitude site in this study could be attributed to the relatively low rainfall experienced at the lower altitude sites compared to the high altitude site on Marion Island (Blake, 1996; le Roux, 2004). Low rainfall areas would be expected to produce leaves with larger specific leaf areas, since smaller leaves are reported to be favored at areas with increased moisture conditions (Bonan, 2002). Rainfall on Marion Island peaks near the upper altitudinal limit of *A. selago* (Blake, 1996; le Roux, 2004), which is the high altitude site on this study. Nyakatya (2006) found little temperature influence on *A. selago* morphology, accounting morphological variation to moisture, light, and wind intensities.

The number of trichomes and trichome density were significantly higher on leaves at the low altitude site than at the other two sites. Previous studies on sub-Antarctic Marion Island reported increasing trichome density with an increase in altitude (le Roux, 2004; Nyakatya, 2006). The opposing trend found on this study was not expected, since trichomes are expected to be more at high altitudes where environmental conditions are less favourable. More trichomes would be a defence mechanism against changes in leaf temperature and moisture, and they would also provide protection against freezing (le Roux, 2004). However, the difference between the altitude of the sites chosen for this study and other previous studies on Marion Island may be the reason for this opposing trend. Previous studies by le Roux (2004) and Nyakatya (2004) showed an apparent increase in trichome density only starting beyond 400 m a.s.l., which was not included on this current study. This altitude (400 m a.s.l.) almost corresponded with the high altitude

site (375 m a.s.l.) for this current study. The adaptive significance of trichome functioning depends on the environment in which they occur (Gutschick, 1999). Trichomes have various functions which would possibly benefit *A. selago* on such an environment as Marion Island. These trichome functions include increasing the rate at which light is captured for photosynthesis at colder higher elevations, by reflection of radiation onto the mesophyl cells (Press, 1999). Furthermore, trichomes reduce water loss by trapping moisture on the leaf surface, also protecting against heat loss through insulation and increase boundary layer thickness (Press, 1999). Trichomes have also been reported in helping to keep leaves dry and keeping stomata unobstructed, thus reducing damage associated with freezing and fungal infections (Halloy and Mark, 1996; Cordell et al., 1998; Press, 1999). Finally, trichomes provide protection against excessive UVB radiation, by shading the leaf surface (Press, 1999).

The effect of shading by *A. magellanica* showed a negative effect on stem growth rate. Exposed stems consistently produced longer and more leaves than shaded stems, however, this difference was only significant for stem length. There were approximately six green leaves on both shaded and exposed stems (see also the comparison on the number of green leaves per altitude site). This agrees with the fact that exposed stems experienced higher growth rates than shaded stems. However, a study on Marion Island reported an opposite trend for non-epiphytic based shading of *A. selago*, with a higher stem growth rate on shaded than exposed plants (le Roux et al., 2005). The results for the current study may be attributed to the larger number of green leaves on exposed stems when compared to shaded stems, therefore resulting in longer stems. This could also suggest that shading by *A. magellanica* has a negative effect on stem growth rate. Another difference between exposed and shaded leaves was the heavier leaves on exposed stems, and higher specific leaf area on shaded stems. The bigger specific leaf area on shaded leaves was expected, since several studies report similar effects of shading on leaf size (Salisbury and Ross, 1992; Havström et al. 1993; Michelson et al. 1996; Niklas, 1996; Cavender-Bares et al. 2000; Dormann and Woodin, 2002; le Roux et al. 2005). The results on this study suggest that leaves under shade have increased leaf light interception area (Lacher, 1980). The number of trichomes stayed the same between exposed and shaded leaves, but the density changed because leaf area changed. However, a previous study on Marion Island reports a lower trichome density on shaded *A. selago*

leaves, thus increasing light interception potential (shading the leaves), while also increasing water loss potential (le Roux et al., 2005).

The abundance and density of the dominant epiphyte, *A. magellanica* on *A. selago*, has previously been shown to decline with altitude on Marion Island (le Roux 2004; Nyakatya 2006). Therefore, the differences found in this study in *A. magellanica* number, and density, as well as the percentage surface area covered by *A. selago* cushions is expected. However, this is the first time that the same trend has been shown for *A. magellanica* off *A. selago* cushions. Also, this study shows that the decline in *A. magellanica* number growing in the fellfield matrix is much more rapid (seen this lower off cushions at mid and high site than at low site) off *A. selago* that on *A. selago* cushions. This suggests that *A. selago* facilitates the growth of *A. magellanica* at higher altitudes. This could be attributed to a milder climate for germination and growth inside *A. selago* cushions compared with the surrounding shallow, undeveloped soil layer. Nyakatya (2006) showed that temperatures inside *A. selago* cushions are warmer and temperature changes dampened compared with the surrounding matrix. Previous alpine studies show high epiphyte abundance associated with cushion plants (Griggs, 1956; Alliende and Hoffmann, 1985; Pyšek, P. and Liška, 1991; Cavieres et al., 1998; Nunez et al., 1999; Molina-Montenegro et al., 2000). Even though some of these studies show facilitation to be more important at higher altitude sites, the abundance of epiphytes growing on cushions is higher at high altitude sites compared to low altitudes (Bertness and Callaway 1994; Brooker and Callaghan, 1998; Callaway and Walker, 1997; Arroyo et al., 2003). This disagrees with the trend shown on this study, where epiphytic *A. magellanica* abundance decreases with altitude. This suggests that in spite of general facilitative effect of *A. selago* on *A. magellanica* towards higher altitudes, the abiotic environmental threshold for *A. magellanica* occurs at lower altitudes than it does for *A. selago*.

Cushions appeared to be green slightly earlier in summer at the low altitude site than at the other sites. This suggests that growth begins earlier at lower altitudes. Flowering also began earlier at the lowest altitude site, and also ended earlier at this site. Nyakatya (2006) also recorded similar results on Marion Island, where flowering was earlier and more rapid at warmer lower altitude site. The size and direction of this

phenological variation in *A. selago* phenology between the three sites could therefore be influenced by the temperature differences between altitude sites.

Azorella selago microclimate temperature, cushion morphology, epiphyte load, and phenology differed between the three sites examined. Some of this variation (especially for *A. magellanica*) appears to be attitudinally related (and associated abiotic conditions), whereas other characteristics (such as leaf morphology) appear to be affected by local habitat conditions, such as topography. This study has also shown that epiphytic growth of *A. magellanica* on *A. selago* regularly affects stem growth rate. This information provides baseline variation trends for understanding the experimental effects of the dominant epiphyte, *A. magellanica* on *A. selago*, reported in the next chapter. Results presented in this chapter also show *A. selago* might be affected by ongoing climate change, if altitude is considered to be an analogue for temperature related consequences of climate change.

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TABLE 1

General description for the three study sites.

Information	Skua Ridge (Low)	Tafelkop (Mid)	Tafelberg (High)
Altitude (m. a. s. l)	103	176	375
Lava type	Grey	Grey	Grey
Slope	Moderate	Gentle	Gentle
GPS position at centre of area	46°51`S, 37°50`E	46°52`S, 37°49`E	46°53`S, 37°47`E

TABLE 2

Azorella selago *cushion size and leaf characteristics [means ± standard errors, and coefficient of variation (%CV) per altitude]. Means of different letters in superscript are significantly different at p < 0.05 (based on an Analysis of Variance). Means are presented from the largest to smallest as is convention for multiple contrasts.*

Variable	Altitude	mean ± s. e	Number of plants	% CV
Cushion size				
Maximum diameter (cm)	High	94.85 ± 4.58[a]	20	28.77
	Middle	63.22 ± 4.58[b]	20	26.70
	Low	60.20 ± 4.58[c]	20	25.27
Perpendicular diameter (cm)	High	54.77± 3.41[a]	20	30.61
	Middle	48.80 ± 3.41[a]	20	29.89
	Low	44.25 ± 3.41[a]	20	32.47
Circumference (cm)	High	325.50 ± 15.01[a]	20	24.88
	Middle	206.95 ± 15.01[b]	20	22.72
	Low	199.45 ± 15.01[b]	20	30.66
Height (cm)	Low	15.29 ± 0.78[a]	20	20.60
	Middle	13.51 ± 0.78[b]	20	30.12
	High	12.43 ± 0.78[ab]	20	25.82
Leaf morphology			Number of stems[*]	
Exposed stem length (cm)[#]	High	1.06 ± 0.04[a]	40	384.77
	Low	0.96 ± 0.04[a]	40	333.22
	Mid	0.70 ± 0.05[b]	25	434.10
Shaded stem length (cm)	Low	0.85 ± 0.03[a]	40	292.20
	High	0.75 ± 0.03[ab]	40	317.22
	Mid	0.66 ± 0.04[b]	25	375.56
No. of leaves on exposed stems	Low	7.22 ± 0.23[a]	40	24.17
	High	6.40 ± 0.23[ab]	40	14.92
	Middle	6.04 ± 0.30[b]	25	29.64

TABLE 2 continued

Azorella selago *cushion morphology and leaf characteristics [means ± standard errors, and coefficient of variation (%CV) per altitude]. Means of different letters in superscript are significantly different at p < 0.05 (based on an Analysis of Variance). Means are presented from the largest to smallest as is convention for multiple contrasts.*

Variable	Altitude	mean ± s. e	Number of stems	%CV
No. of leaves on shaded stems	Middle	6.60 ± 0.31^{a}	25	33.87
	Low	6.25 ± 0.25^{a}	40	25.55
	High	6.17 ± 0.25^{a}	40	15.51
Exposed leaf mass (g) #	High	0.011 ± 0.01^{a}	40	60.55
	Middle	0.003 ± 0.01^{b}	25	55.61
	Low	0.008 ± 0.01^{a}	40	48.16
Shaded leaf mass (g)	High	0.007 ± 0.0004^{a}	40	54.83
	Low	0.006 ± 0.0004^{a}	40	28.93
	Middle	0.003 ± 0.0005^{b}	25	65.14
Exposed leaf area (mm^2) #	High	31.09 ± 1.49^{a}	40	39.10
	Low	28.95 ± 1.49^{a}	40	27.52
	Middle	21.66 ± 1.89^{b}	25	27.50
Shaded leaf area (mm^2) #	High	28.49 ± 1.08^{a}	40	30.62
	Low	22.53 ± 1.08^{b}	40	24.94
	Middle	20.33 ± 1.37^{b}	25	24.71
Exposed specific leaf area ($mm^2.g^{-1}$)	Middle	5958.88 ± 449.39^{a}	25	41.70
	Low	4092.28 ± 355.28^{b}	40	47.13
	High	3505.44 ± 355.28^{b}	40	64.56
Shaded specific leaf area ($mm^2.g^{-1}$) #	Mid	7352.26 ± 590.40^{a}	25	45.64
	High	$53.70.62 \pm 466.75$	40	70.56
	Low	3527.98 ± 466.75^{c}	40	34.71
Exposed trichome no. #	Low	11.45 ± 0.47^{a}	40	24.29
	Middle	9.40 ± 0.60^{b}	25	31.31
	High	8.65 ± 0.47^{b}	40	37.80
Shaded trichome no. #	Low	11.30 ± 0.42^{a}	40	21.50

TABLE 2 continued

Azorella selago *cushion morphology and leaf characteristics [means ± standard errors, and coefficient of variation (%CV) per altitude]. Means of different letters in superscript are significantly different at p < 0.05 (based on an Analysis of Variance). Means are presented from the largest to smallest as is convention for multiple contrasts.*

Variable	Altitude	mean ± s. e	Number of stems	%CV
Shaded trichome no. [#]	Middle	9.40 ± 0.54^{b}	25	32.78
	High	9.00 ± 0.42^{b}	40	30.19
Exposed trichome density (per mm^2) [#]	Low	0.82 ± 0.04^{a}	25	38.45
	Middle	0.74 ± 0.05^{ab}	40	34.46
	High	0.60 ± 0.04^{b}	40	48.33
Shaded trichome density (per mm^2) [#]	Low	0.96 ± 0.04^{a}	40	31.35
	Middle	0.81 ± 0.06^{ab}	25	42.33
	High	0.68 ± 0.04^{b}	40	43.59

[*]*. 40 stems = 5 stems on 8 plants and 25 stems = 5 stems on 5 plants*

[#]*. log transformed prior to analysis.*

TABLE 3

Comparison of stem growth and leaf characteristics between cushions covered with A. magellanica *and those without, controlling for between altitude site differences described in text (based on an Analysis of Variance).*

Overall model results		Independent factors			
		Altitude site		Exposed and Shaded	
F (d. f.)	p	F(d. f)	p	F(d. f)	p
Stem length					
17	<0.001	10.51	<0.001	23	<0.001
(3, 206)		(2, 206)		(1, 206)	
Leaf number					
2.09	0.1	1.8	0.16	2.67	0.1
(3, 206)		(2, 206)		(1, 206)	
Leaf mass					
35.62	<0.001	45.25	<0.001	16.36	<0.001
(3, 206)		(2, 206)		(1, 206)	
Leaf area					
14.52	<0.001	17.16	<0.001	9.24	<0.05
(3, 206)		(2, 206)		(1, 206)	
Specific leaf area					
14.77	<0.001	19.74	<0.001	4.82	<0.05
(3, 206)		(2, 206)		(1, 206)	
Trichome no.					
10.30	<0.001	15.13	<0.001	0.59	0.44
(3, 205)		(2, 205)		(1, 205)	
Trichome density					
10.30	<0.001	13.15	<0.001	6.04	<0.05
(3, 206)		(2, 206)		(1, 206)	

TABLE 4

Azorella selago *stem and leaf characteristics between exposed and shaded cushions [means ± standard errors, and coefficient of variation (%CV) per altitude site]. Means of different letters are significantly different at $p < 0.05$ (based on an Analysis of Variance). Means are presented from the largest to smallest as is convention for multiple contrasts.*

Variable	Exposed/Shaded	mean ± s. e	Number of stems*	% CV
Stem length (cm) #	Exposed	0.94 ± 0.028^{a}	105	322.56
	Shaded	0.76 ± 0.024^{b}	105	299.97
Leaf number#	Exposed	6.62 ± 0.15^{a}	105	422.06
	Shaded	6.30 ± 0.15^{a}	105	400.09
Leaf mass (g) #	Exposed	0.0086 ± 0.0005^{a}	105	149.89
	Shaded	0.006 ± 0.0003^{b}	105	189.68
Leaf area (mm^2) #	Exposed	28.03 ± 0.95^{a}	105	278.19
	Shaded	24.28 ± 0.74^{b}	105	318.89
Specific leaf area ($mm^2.g^{-1}$) #	Shaded	5140.48 ± 319.86^{a}	105	156.83
	Exposed	4325.97 ± 232.56^{b}	105	181.52
Trichome no.#	Shaded	9.97 ± 0.28^{a}	105	346.17
	Exposed	9.89 ± 0.31^{a}	105	305.39
Trichome density (per mm^2)	Shaded	0.82 ± 0.032^{a}	105	248.68
	Exposed	0.72 ± 0.029^{b}	105	235.28

**. 105 stems = 21 leaves on 5 on stems*

#. log transformed prior to analysis

TABLE 5

Characteristics of the dominant epiphyte on and off Azorella selago, *i.e.* Agrostis magellanica *[means ± standard deviations] and coefficient of variation (%CV), n = 100; and* A. selago *vitality [median (range), n = 30]. Means with different letters in superscript are significantly different at p < 0.05 (based on an Analysis of Variance). Means are presented from the largest to smallest as is convention for multiple contrasts.*

Variable	Altitude	Mean ± s. d	%CV
Epiphyte load			
Agrostis number (on cushions)*	Low	195.9 ± 262.5[a]	133.99
	Mid	144.91 ± 87.05[a]	129.08
	High	90.3 ± 162.19[b]	179.62
Agrostis density (no. per cm^2) *	Low	0.47 ± 0.37[a]	77.858
	Mid	0.44 ± 0.63[a]	143.15
	High	0.16 ± 0.22[b]	136.91
Agrostis number (off cushions)	Low	34.1 ± 14.79[a]	43.396
	Mid	17.1 ± 6.98[b]	40.835
	High	4.40 ± 6.93[c]	157.53
		Median (range)	
Agrostis cover (%)	Low	40 (1 - 95)	
	Mid	30 (0 – 80)	
	High	20 (0 – 70)	
Cushion vitality	Low	6.0 (2 – 10)	
	Mid	6.5 (3 – 8.0)	
	High	7.0 (3 – 10)	

*. *log transformed prior to analysis*

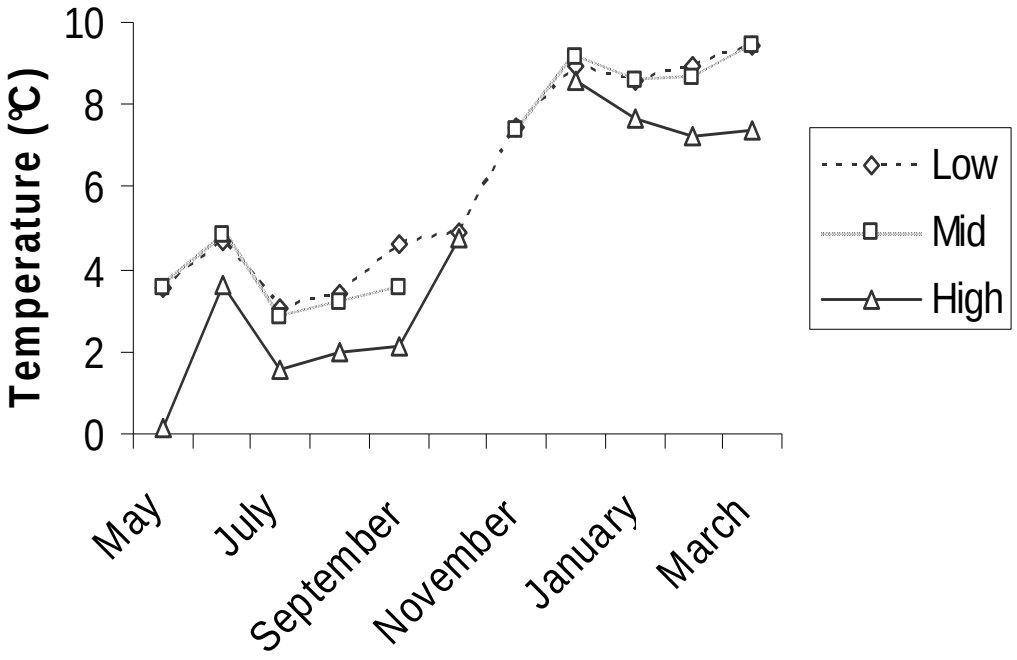


FIGURE 1. Azorella selago *microclimate mean temperatures at three altitudes for the given months (n = 5 plants at each altitude, error bars excluded for clarity, see details in Appendix A).*

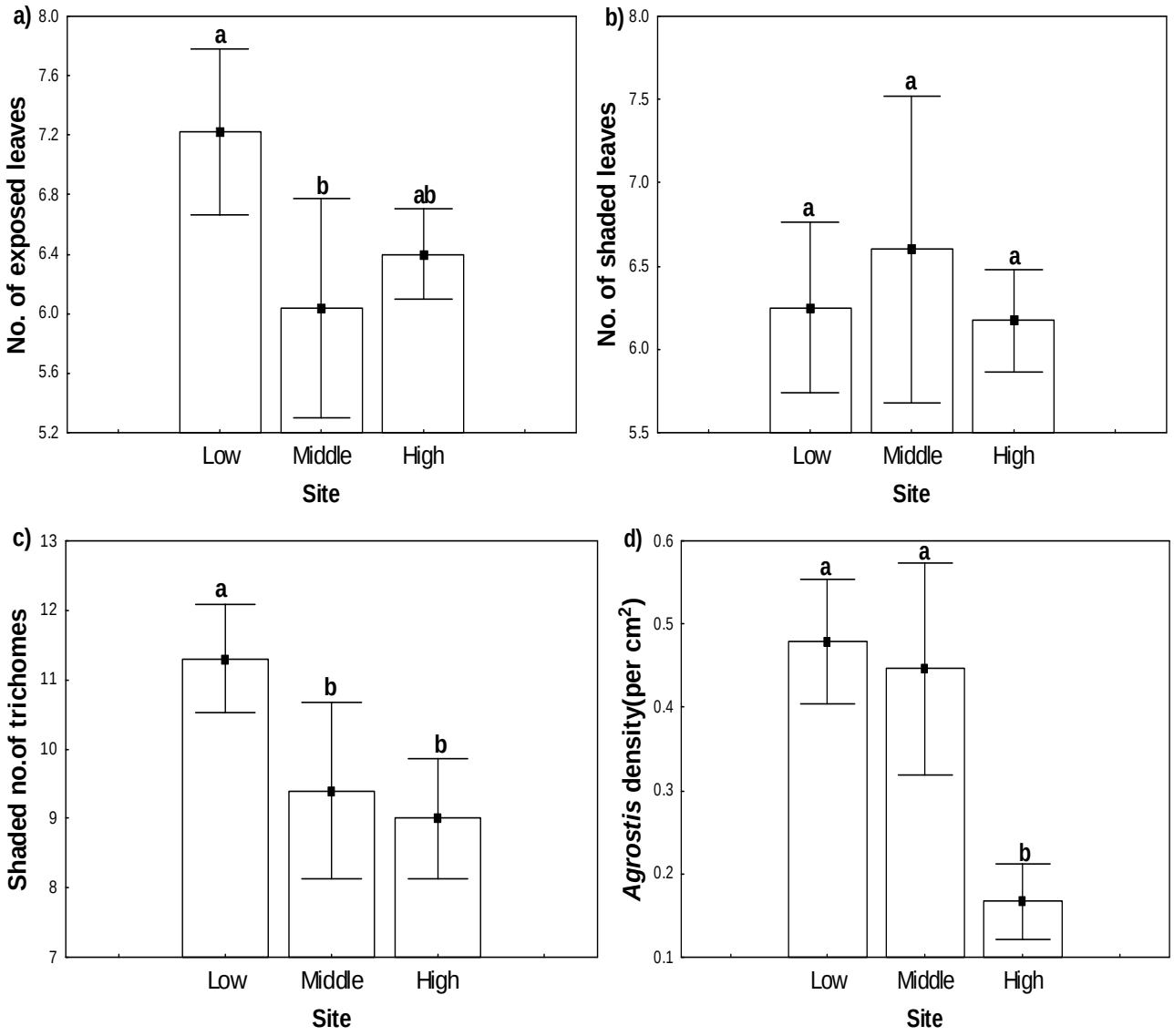
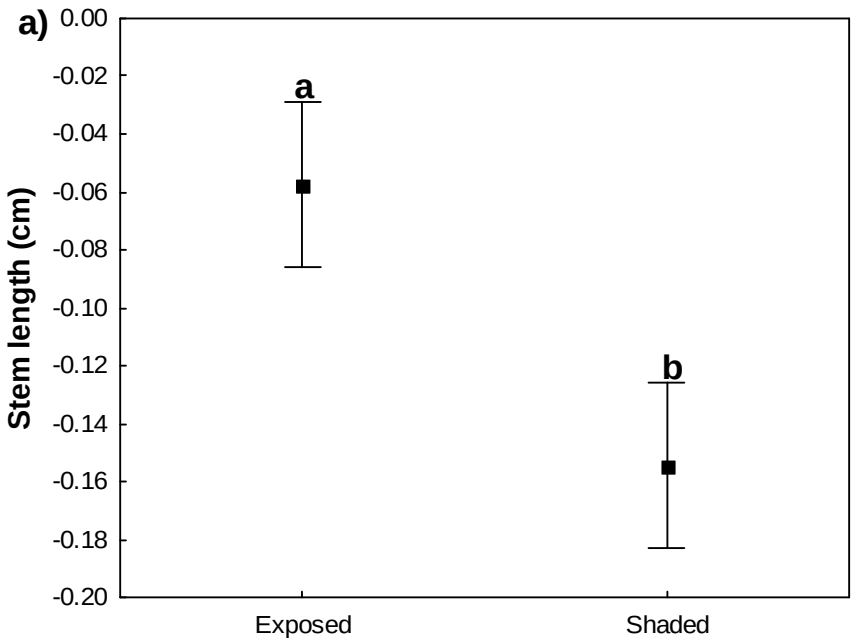
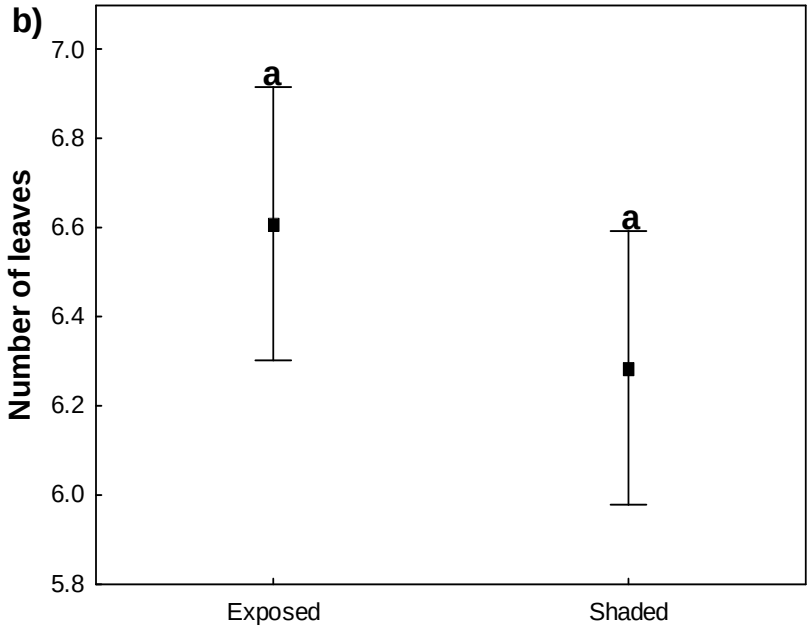
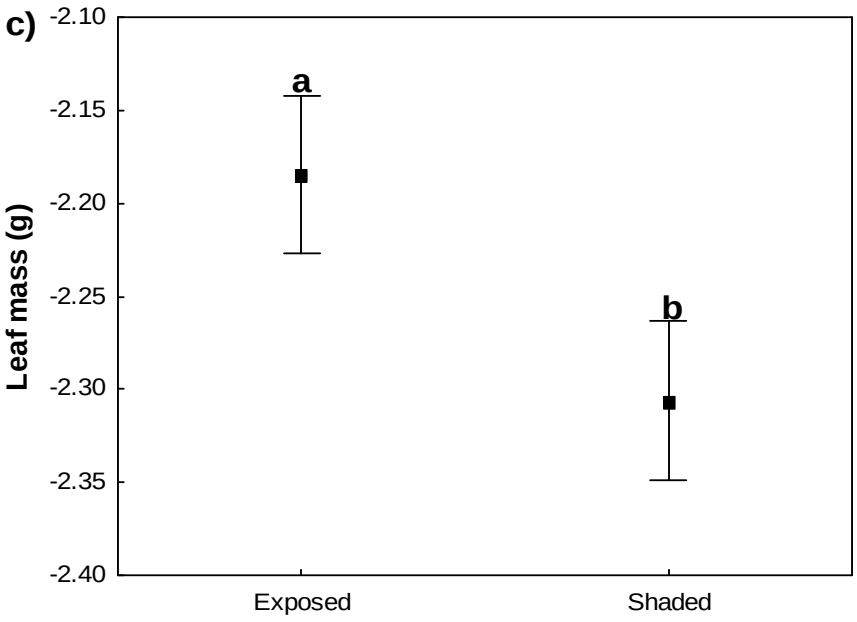
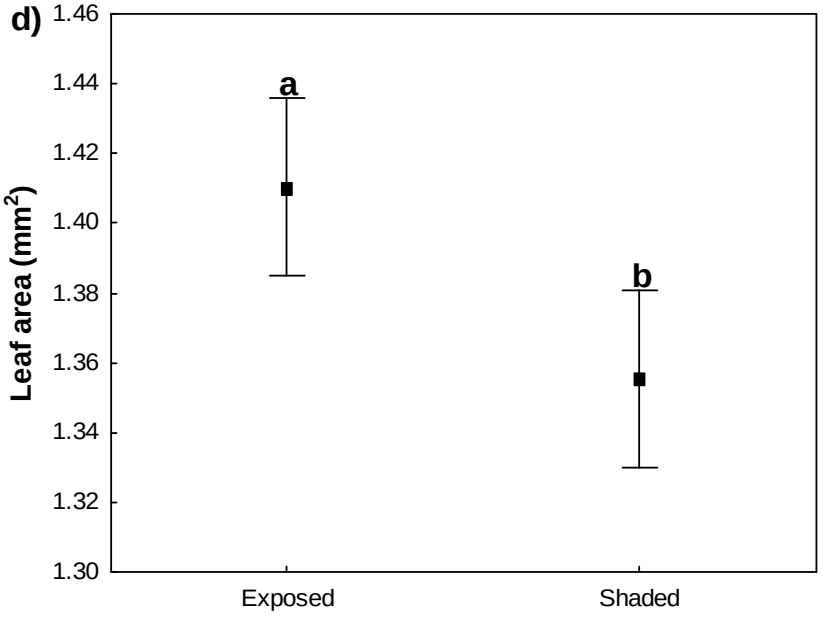


FIGURE 2. Azorella selago *leaf morphology (mean ± 0.95 confidence interval) at three altitudes (i.e. low, middle and high); a) number of green leaves on exposed stems, b) number of green leaves on shaded stems, c) number of trichomes on shaded leaves and d)* Agrostis magellanica *density. Means with different letters are significantly different at $p < 0.05$ (based on an Analysis of Variance).*


a)
Stem length (cm)
0.00
-0.02
-0.04
-0.06
-0.08
-0.10
-0.12
-0.14
-0.16
-0.18
-0.20
a
b
Exposed
Shaded


b)
Number of leaves
7.0
6.8
6.6
6.4
6.2
6.0
5.8
a
a
Exposed
Shaded


c)
-2.10
-2.15
-2.20
-2.25
-2.30
-2.35
-2.40
Leaf mass (g)
a
b
Exposed
Shaded


d)
1.46
1.44
1.42
1.40
1.38
1.36
1.34
1.32
1.30
Leaf area (mm2)
a
b
Exposed
Shaded

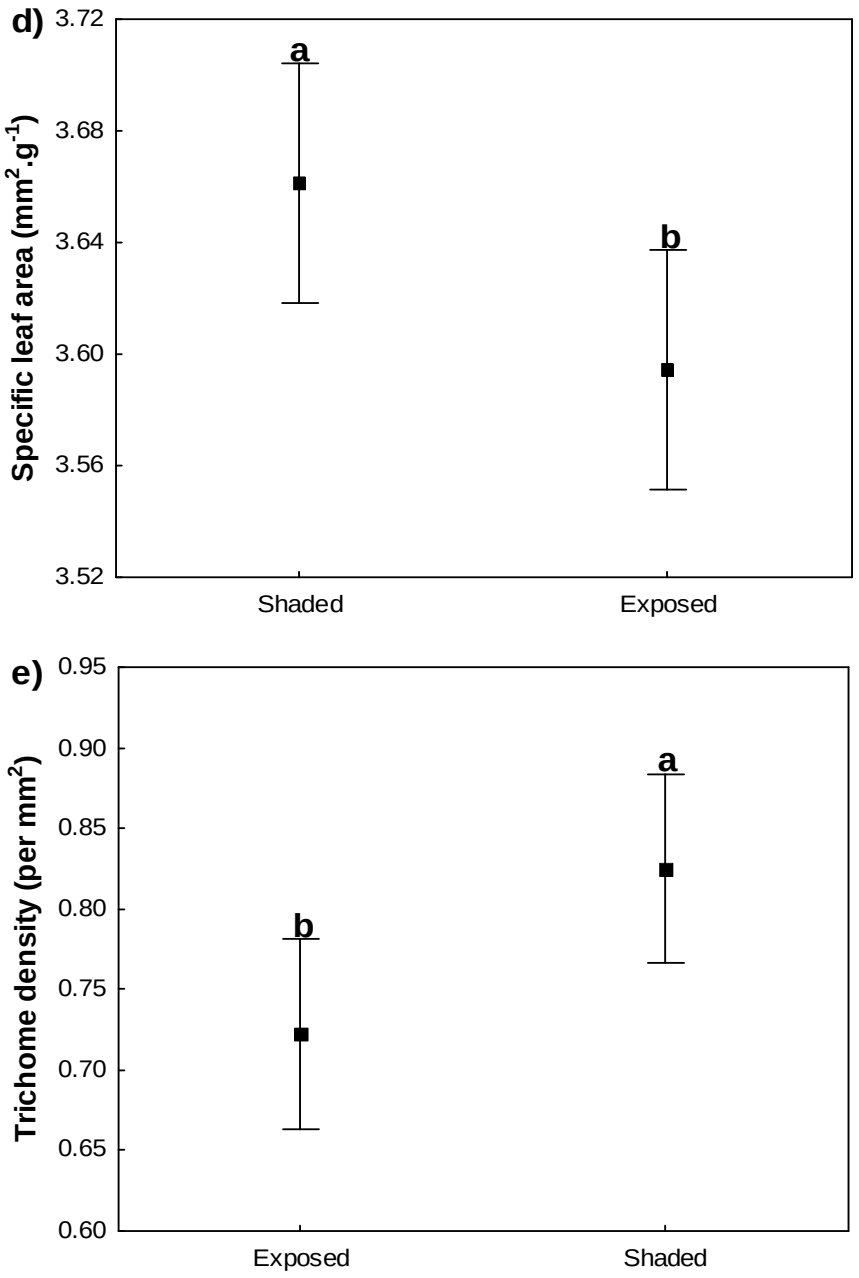


FIGURE 3. Azorella selago *stem and leaf characteristics (mean ± 95% Confidence Interval) between exposed and shaded cushions; a) stem length, b) leaf number, leaf mass, c) leaf area, d) specific leaf area, e) trichome density. Means with different letters are significantly different at $p < 0.05$ (based on an Analysis of Variance).*

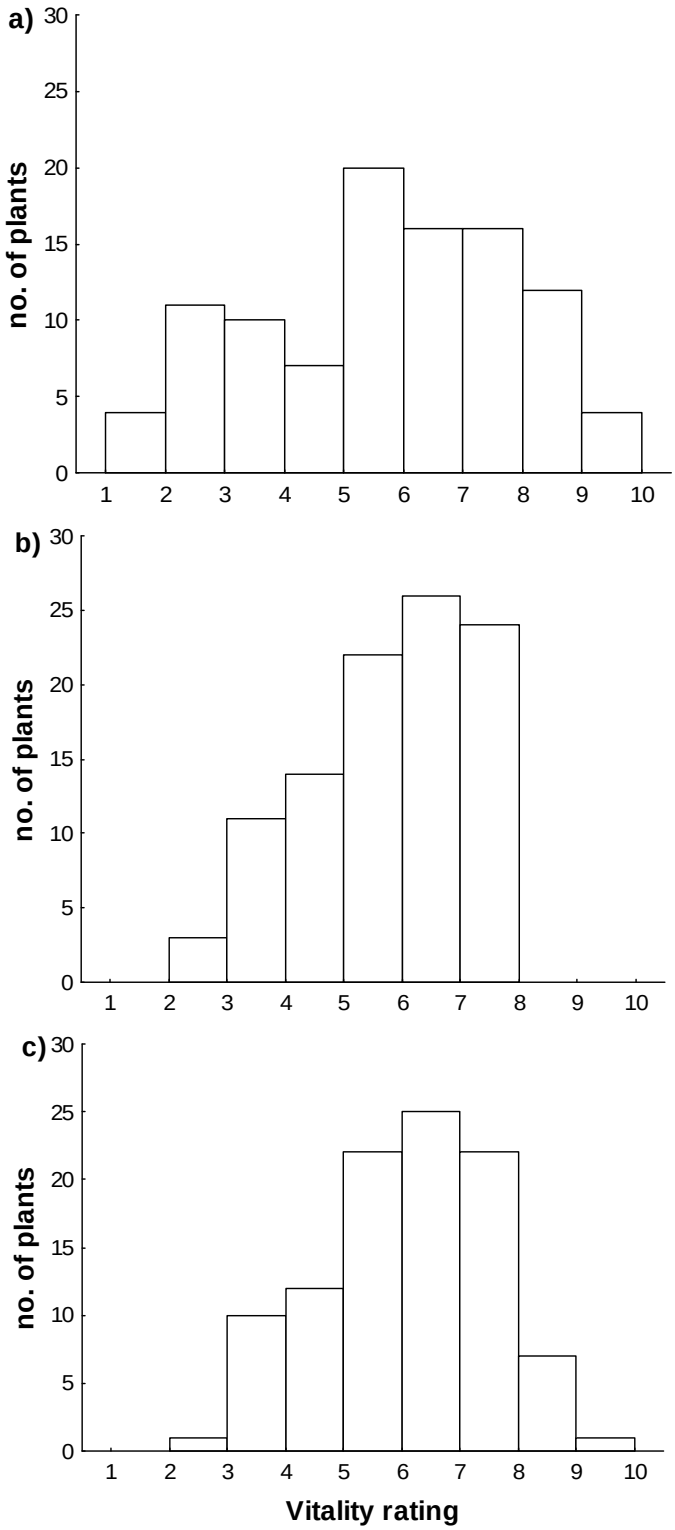


FIGURE 4. Azorella selago *vitality frequency distributions at three altitudes, i.e. (a) low, (b) mid, (c) high altitude site, (n = 100). Vitality ranking between 1 (low vitality) – 10 (high vitality).*

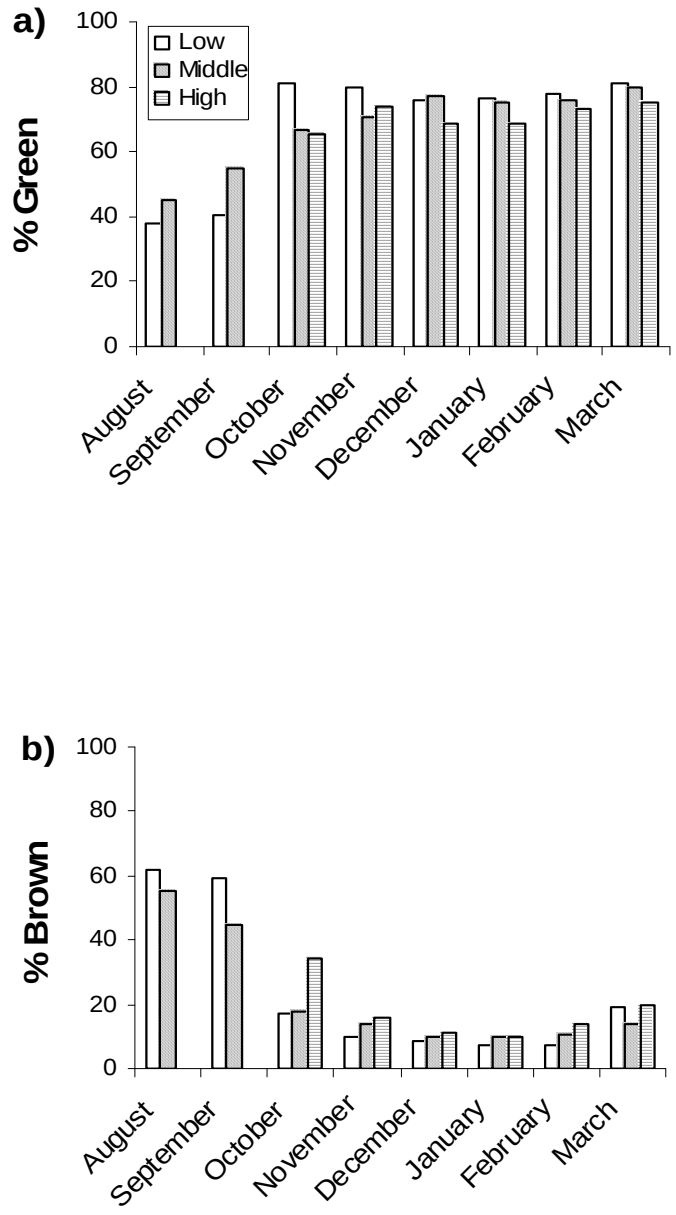


FIGURE 5. Phenology of Azorella selago *plants at low, middle and high altitudes (a) median % green, (b) % brown plant surface area (n = 20). (No data collected at the high altitude site in August and September due to snow cover on cushions).*

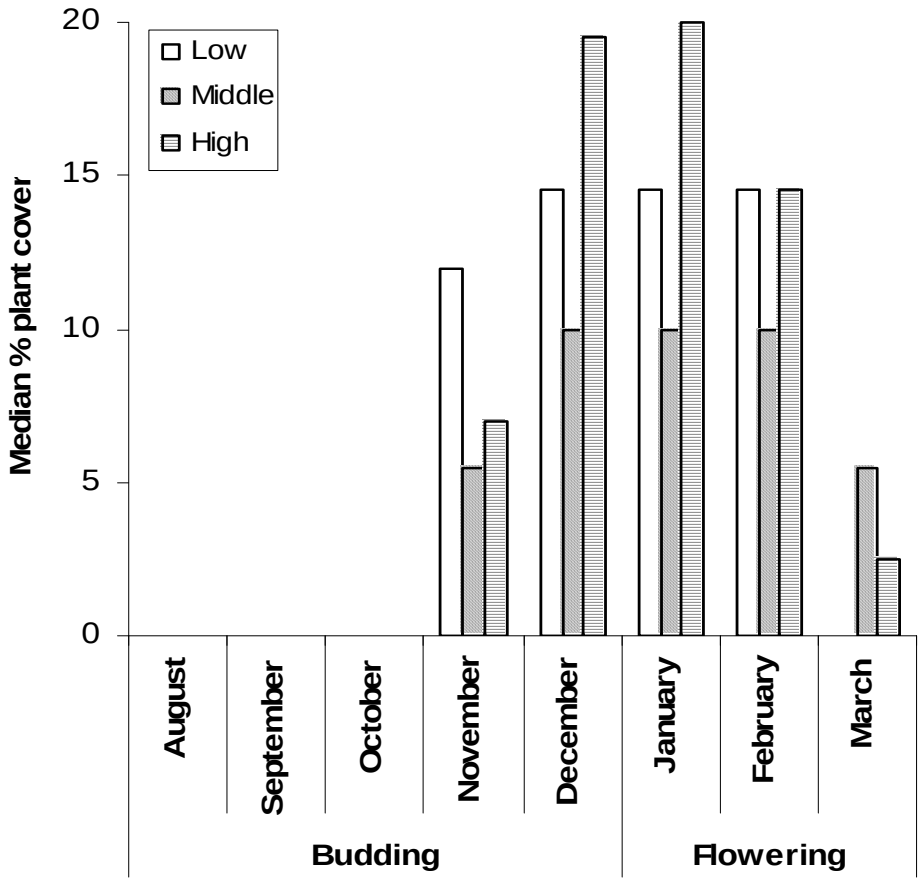
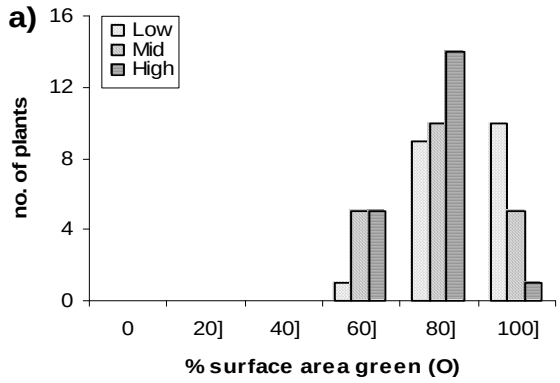
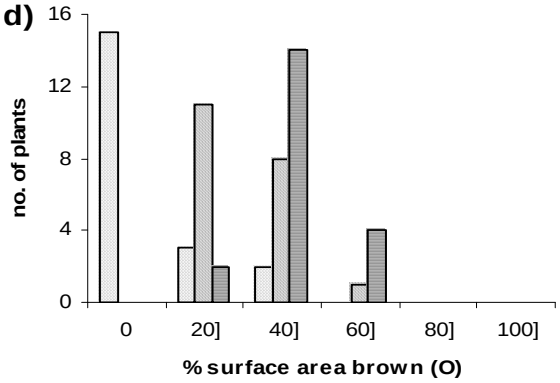
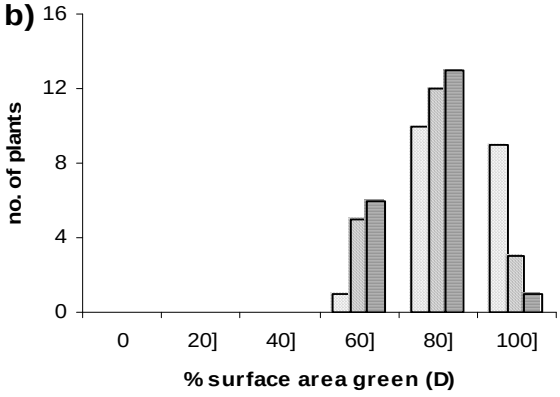
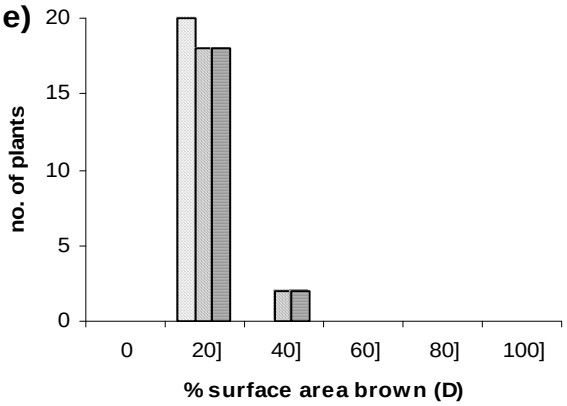


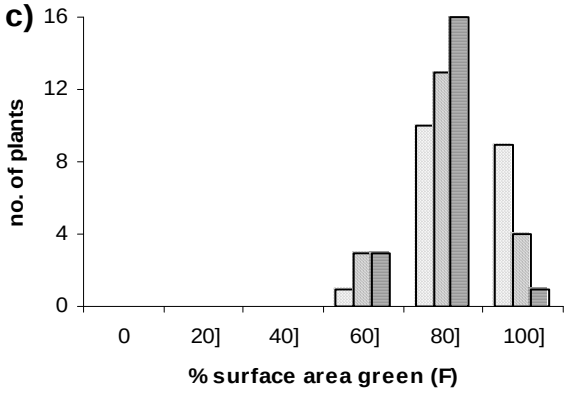
FIGURE 6. Azorella selago *median % flower budding and % flowering plant surface area at low, middle and high altitude sites (n = 20).*

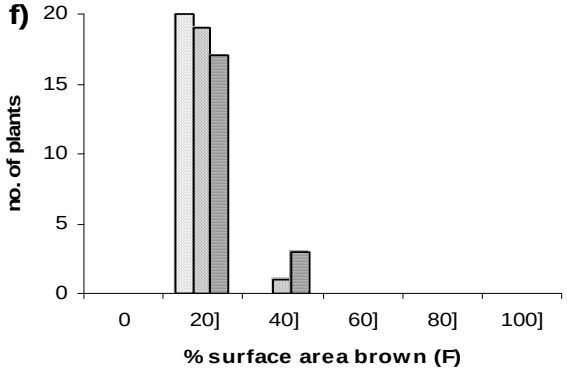

a)
Low
Mid
High
no. of plants
0
4
8
12
16
0
20]
40]
60]
80]
100]
% surface area green (O)


d)
no. of plants
0
4
8
12
16
0
20]
40]
60]
80]
100]
% surface area brown (O)


b)
no. of plants
0
4
8
12
16
0
20]
40]
60]
80]
100]
% surface area green (D)


e)
no. of plants
0
5
10
15
20
0
20]
40]
60]
80]
100]
% surface area brown (D)


c)
no. of plants
0
4
8
12
16
0
20]
40]
60]
80]
100]
% surface area green (F)


f)
no. of plants
0
5
10
15
20
0
20]
40]
60]
80]
100]
% surface area brown (F)

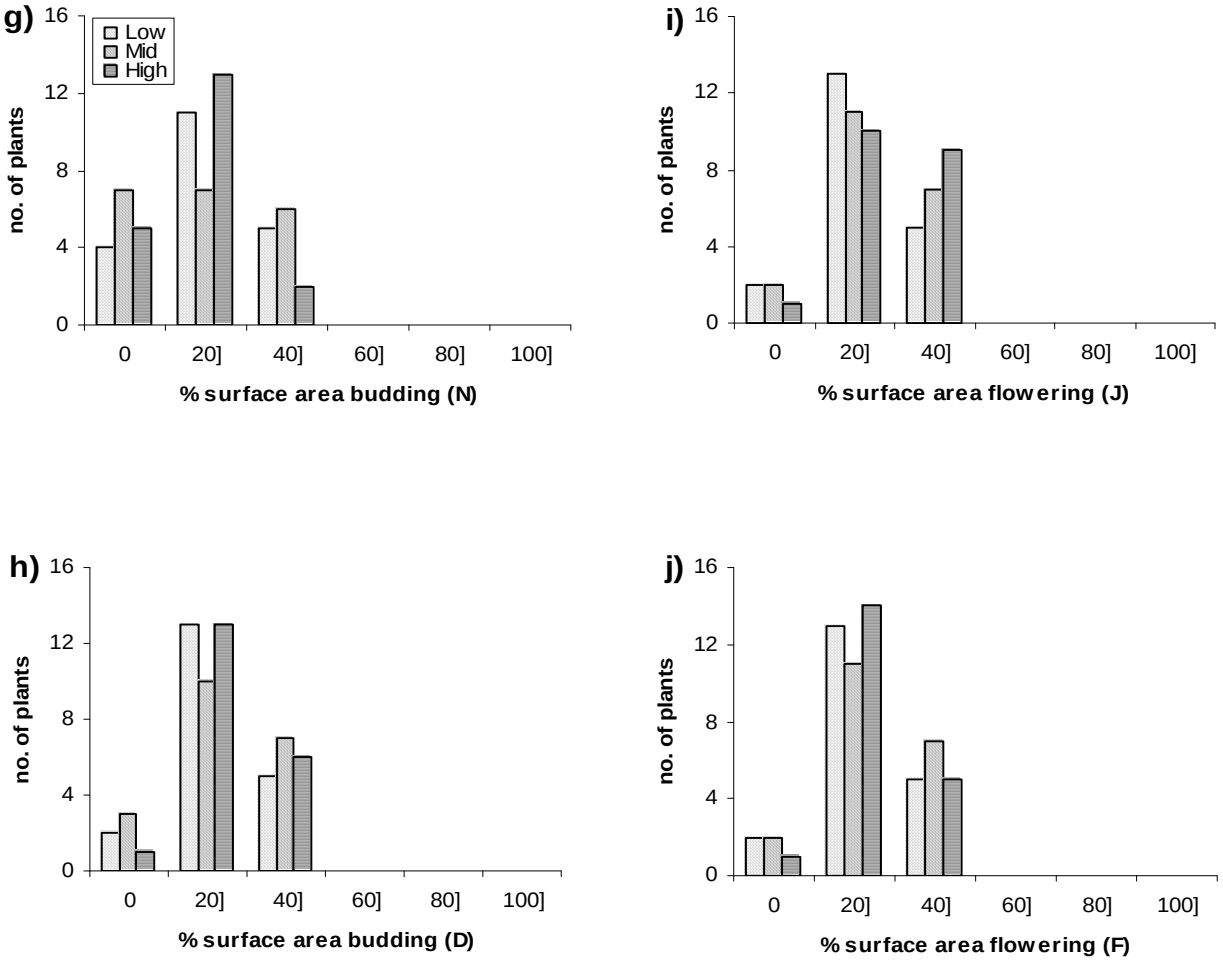


FIGURE 7. Frequency distribution of median surface area (%) of cushions that were brown, green, budding, and flowering for those months measured in which phenological trait was present (J = January, F = February, N = November, D = December, O = October) (n = 20).

APPENDIX A

Daily mean temperatures (℃) at three altitudes, [Treatment (see Chapter 2): 1 = plants with high Agrostis magellanica *abundance, 6 = plants with low* A. magellanica *abundance].*

Altitude	Treatment	Mean (± s. d)	Min	Max	N (days)
May:					
Low	1	3.58 ± 2.60	0	12.5	18
	6	3.52 ± 2.54	-4	11.5	19
Mid	1	3.33 ± 3.01	0	10.5	5
	6	3.53 ± 3.08	-5	10.5	5
High	1	0.67 ± 0.29	0	5.0	2
	6	0.16 ± 0.15	-1	2.0	2
June:					
Low	1	4.70 ± 2.54	-0.5	11.5	30
	6	4.68 ± 2.59	-0.5	11.0	30
Mid	1	4.48 ± 2.64	-0.5	11.5	30
	6	4.80 ± 2.59	-0.5	11.0	30
High	1	3.83 ± 2.53	-0.5	10.5	30
	6	3.65 ± 2.80	-1	11.5	30
July:					
Low	1	3.13 ± 2.36	-2	8.5	31
	6	3.06 ± 2.42	-1.5	8.0	31
Mid	1	2.66 ± 2.22	-1.5	7.5	31
	6	3.87 ± 2.21	-2	7.5	31
High	1	2.05 ± 1.81	0	6.5	31
	6	1.56 ± 2.00	-2	7.0	31
August:					
Low	1	3.49 ± 2.71	-1.5	11.0	31
	6	3.40 ± 2.75	-1	10.5	31
Mid	1	3.01 ± 2.60	-1	11.0	31

APPENDIX A continued

Daily mean temperatures (℃) at three altitudes, [Treatment (see Chapter 2): 1 = plants with high Agrostis magellanica *abundance, 6 = plants with low* A. magellanica *abundance].*

Altitude	Treatment	Mean (± s. d)	Min	Max	N (days)
Mid	6	3.22 ± 2.55	-1	10.0	31
High	1	2.36 ± 2.32	-1.5	13.5	31
	6	2.01 ± 2.59	-2	12.5	31
September:					
Low	1	4.71 ± 3.73	-0.5	19.0	10
	6	4.63 ± 4.39	-0.5	19.0	10
Mid	1	3.41 ± 3.73	-1	17.5	24
	6	3.57 ± 3.53	-1	17.5	24
High	1	3.37 ± 2.50	-2	16.5	30
	6	2.13 ± 2.82	-2	15.0	30
October:					
Low	1	4.75 ± 2.61	0	18.0	9
	6	4.85 ± 2.37	0	10.5	9
High	1	4.88 ± 3.21	-0.5	17.5	31
	6	4.78 ± 3.73	-1	18.0	31
Nov:					
Low	1	7.52 ± 3.68	0.5	23.0	30
	6	7.41 ± 3.38	0.5	21.0	30
Mid	1	7.21 ± 3.45	1	20.0	30
	6	7.36 ± 3.56	1.5	18.5	30
December:					
Low	1	9.14 ± 3.61	1.5	25.5	31
	6	8.96 ± 3.21	1	22.0	31
Mid	1	9.11 ± 3.66	1.5	23.0	31
	6	9.14 ± 3.71	1.5	21.5	31
High	1	8.68 ± 3.91	2	22.5	14

APPENDIX A continued

Daily mean temperatures (℃) at three altitudes, [Treatment (see Chapter 2): 1 = plants with high Agrostis magellanica *abundance, 6 = plants with low* A. magellanica *abundance].*

Altitude	Treatment	Mean (± s. d)	Min	Max	N (days)
High	6	8.57 ± 4.27	1.5	23.0	14
January:					
Low	1	8.89 ± 3.73	1	24.5	31
	6	8.60 ± 3.35	1	22.5	31
Mid	1	8.62 ± 3.63	1.5	22.0	31
	6	8.61 ± 3.67	1.5	21.0	31
High	1	7.96 ± 3.60	0	21.5	31
	6	7.63 ± 3.96	0	22.5	31
February:					
Low	1	9.17 ± 3.55	1.5	26.0	28
	6	8.94 ± 3.10	1.5	21.0	28
Mid	1	8.63 ± 3.18	1	20.0	28
	6	8.63 ± 3.21	1.5	20.0	28
High	1	7.57 ± 3.08	1.5	19.5	28
	6	7.22 ± 3.38	0	21.0	28
March:					
Low	1	9.38 ± 4.78	1	26.5	20
	6	9.41 ± 4.79	0.5	26.0	20
Mid	1	9.36 ± 4.71	1	21.5	11
	6	9.40 ± 4.50	1	20.5	11
High	1	7.69 ± 3.83	-5	20.5	14
	6	7.40 ± 3.96	0	20.0	14

APPENDIX B

Phenological traits for 10 control Azorella selago *plants with low* Agrostis magellanica *abundance per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Aug 2004	38.7 (20 - 48)	42.0 (21 - 50)	_	61.3 (52 - 80)	57.0 (42 - 79)	-	0	0	-	0	0	-
Sept 2004	40.9 (20 - 50)	58.3 (40 - 80)	_	59.1 (50 - 80)	41.7 (16 - 60)	-	0	0	-	0	0	-
Oct 2004	77.3 (62 - 90)	63.0 (47 - 82)	66.4 (56 - 82)	18.6 (7 - 40)	18.3 (6 - 38)	34.6 (25 - 44)	4.1 (0 - 24)	18.7 (0 - 39)	0	0	0	0
Nov 2004	79.1 (61 - 90)	66.0 (50 - 70)	70.3 (60 - 80)	9.0 (2 - 20)	14.0 (5 - 30)	18.9 (10 - 40)	11.19 (3 - 29)	20.0 (0 - 40)	10.8 (0 - 30)	0	0	0
Dec 2004	77.8 (75 - 85)	67.2 (53 - 80)	64.0 (50 - 78)	9.4 (3 - 20)	9.9 (5 - 20)	12.5 (4 - 25)	14.0 (0 - 29)	22.9 (0 - 40)	19.5 (10 - 30)		0	4.0 (0 - 11)

APPENDIX B continued

Phenological traits for 10 control Azorella selago *plants with low* Agrostis magellanica *abundance per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
	Low	High	Mid	Low	Mid	High	Low	Mid	High	Low	Mid	High
Jan 2005	77.8 (75 - 85)	67.3 (53 - 81)	64.5 (55 - 78)	12.34 (3 - 20)	9.6 (5 - 20)	12.5 (4 - 25)	0	0	0	14.0 (0 - 29)	23.1 (0 - 40)	23.0 (12 - 30)
Feb 2005	78.1 (75 - 85)	68.6 (56 - 81)	67.4 (59 - 78)	8.6 (3 - 20)	10.6 (5 - 20)	13.9 (4 - 27)	0	0	0	13.3 (0 - 29)	20.8 (0 - 35)	18.7 (0 - 35)

Chapter 3: Ecological impact of epiphytic *Agrostis magellanica* on its host plant *Azorella selago* (Apiaceae)

Introduction

Plant interactions play a vital role in structuring of plant communities and in changes occurring within these communities (Kikvidze et al., 2001; Cavieres et al., 2006). Epiphytic interactions are good models for studying plant interactions, since host plants and the plant community as a whole may be affected in various ways. For example microclimate, phenology and reproduction activities, as well as morphology of plants could be affected by long-term shading from epiphytes. Previous studies on cushion plants (plants with a hard, compact cushion growth form, Orchard, 1989), report warmer, as well as humid, favourable temperatures within cushions compared with the surrounding environment, promoting seed germination for epiphyte species (Griggs 1956; Alliende and Hoffmann, 1985; Pyšek and Liška, 1991; Cavieres et al., 1998; Korner, 1999; Nunez et al., 1999; Molina-Montenegro et al., 2000; Cavieres et al., 2002; Arroyo et al., 2003; Nyakatya, 2006). Phenological stages could also be altered on plants growing under sheltered environments, for example, plants growing in sheltered environments have longer growing seasons as well as larger leaves (Huntley, 1972; Frenot et al., 1993; le Roux et al., 2005). In cushion plants in particular, shading through heavy epiphyte densities also increases the extent of dead, loosely packed stems leading to stem mortality (Bergström et al., 1997; Shaver et al., 1998; le Roux, et al., 2005).

Epiphytic relationships between plants can vary between positive and negative, depending on how these interactions vary in strength and direction (Stone and Roberts, 1991; Miller, 1994; Berlow, 1999; Levine, 1999). The relative importance of competition, which is a negative interaction, decreases with increasing facilitation and abiotic stress (Brooker and Callaghan, 1998). This often results in low epiphyte densities at low altitudes when compared to high altitudes. There are various factors influencing facilitation and competition in plant communities. For example, moisture conditions within the host plant, substrate quality, microclimate, and nutrient availability affect the colonization of epiphytes (Hietz and Briones, 1998; Choler et al., 2001; Zotz and Hietz,

2001; Callaway et al., 2002). Previous studies showed that positive and negative spatial associations are influenced by altitude (Callaway and Walker, 1997, Choler et al., 2001, Cavieres et al., 2006); hence temperature is one factor which has a great influence on plant interactions. Temperature differs with changes in elevation (Blake, 1996; Boelhouwers, 2003; Holnes, 2003; Nyakatya, 2006).

Several studies have proposed that positive interactions between plant species are more likely to be observed in harsh, stressful environments (Bertness and Callaway, 1994; Callaway and Walker, 1997; Brooker and Callaghan, 1998; Cavieres et al., 2002; Bruno et al., 2003). This is attributed to the fact that resources for plants may be limited in harsh environments, and any presence of a neighbour will favour growth until it outweighs the negative, competitive impact of growing in close associations (Brooker and Callaghan, 1998; Bruno et al., 2003). Positive interactions have been reported between cushion plants and epiphytes in alpine environments (Griggs 1956; Allende and Hoffmann, 1985; Nunez et al., 1999; Molina-Montenegro et al., 2000; Badano et al., 2002; Cavieres et al., 2002; Arroyo et al., 2003). All these studies provided evidence showing that cushions plants act as nurse plants, providing favorable conditions for the recruitment of other species. Cavieres et al. (2006) studied the spatial association of plant species with the cushion *Laretia acaulis* at two different elevations, where there was a high seed survival within cushions at low altitudes. This suggests that the importance of positive association is more important at lower altitudes than at high altitudes, where epiphyte density is low. Previous studies on sub-Antarctic Marion Island show more epiphyte species growing on *Azorella selago* cushions at low altitudes (le Roux, 2004; Nyakatya, 2006). However, this was in contrast with other studies where a consistent finding being a positive correlation of positive associations with altitude (Cavieres et al., 2002; Arroyo et al., 2003).

High latitude communities provide good sites for studying the importance of positive and negative interactions along an altitudinal gradient (Choler et al., 2001). They have simple systems where changes are easily detected in various stressors and disturbances (Choler et al., 2001; Callaway et al., 2002; Cavieres et al., 2006). An altitudinal gradient is associated with changes in temperature, precipitation, intensity in solar radiation, partial pressure of atmospheric gases and vapor pressure gradients often

across relatively short distances (Bowman et al., 1999, Cavieres et al., 2000). Studying these altitudinal gradients offers an analog for future climates (Hodkinson and Bird, 1998; Hodkinson and Wookey, 1999). For example, studying plants at warmer, lower altitudes serves as an analog for the potential response of plants currently at cooler high altitude sites to increased temperature. Similarly, the analog can also be applied to a cooling scenario, where high altitudes may be regarded as a predictor of low altitude conditions (Tweedie and Bergström, 2000). This method can also be applied when studying plant-epiphytic interactions at different altitude areas.

Prince Edward Islands in the Southern Ocean are suitable ecosystems for studying plant interactions and how they may change as a consequence of climate change. These ecosystems are remote, closed systems, with harsh environments accommodating low species richness which are often vulnerable to change (Smith and Steenkamp, 1990; Callaghan et al., 1992; Davies and Melbourne, 1999). Marion Island, which is relatively larger than the small Prince Edward is an example of such a system. The island is situated 1770 km south of South Africa and is part of the Prince Edward Island group (Hänel and Chown, 1998). The plant biota of Marion Island includes 22 indigenous vascular plants, approximately 80 mosses, 36 liverworts, and 50 lichens (Gremmen et al., 1998). Vascular plants occur over a wide range of habitats and have wide altitudinal limits (Smith and Steenkamp, 1990).

Azorella selago Hook.f. (Apiaceae) covers the largest altitudinal range of vascular plants across Marion Island (Huntley, 1970; le Roux and McGeoch, 2004). An experiment simulating current climate change trends was recently conducted on Marion Island to study the effects of reduced rainfall and increased temperature on *A. selago* (le Roux, et al., 2005). Continued warming and drying of the island will potentially cause this cushion to move to higher altitudes, although also shortening it growing season and causing increased rates of dieback (le Roux et al., 2005). The dominant epiphyte on *A. selago*, *Agrostis magellanica* Lam. (Poaceae) might also be affected. Warming alone could cause an increase in abundance of most epiphyte species (le Roux et al., 2005), also expanding their altitudinal ranges upslope. This would bring about much heavier shading on *A. selago* by more rapidly growing vascular species, leading to a short-term increase in stem mortality under longer-term shading (le Roux et al., 2005). However, the nature

of the interaction between *A. selago* and *A. magellanica* has never been directly examined, and the impact of the grass on cushions plants remains poorly understood.

The objectives of this study were to quantify the effect of the dominant epiphyte, *A. magellanica* on biotically-relevant microclimatic temperatures, as well as on the phenology and physical condition of *A. selago*. The three study sites chosen at different altitudes, described in Chapter 1, were also used to understand the effect of the dominant epiphyte on *A. selago* in this Chapter. Studying plants across altitudes provides a possible analogue of the temperature-related climate change consequences on the ecology of *A. selago* and the interaction with *A. magellanica*, its dominant epiphyte species. Temperatures at higher altitudes are relatively colder, and ongoing climate change is predicted to cause an upward shift in the distribution of vascular plant species on Marion Island. Climate change may also affect the interaction between *A. selago* and *A. magellanica*, which has never been directly examined on Marion Island.

Materials and methods

SPECIES DESCRIPTION AND HABITAT

Azorella selago is a cushion forming herbaceous dominant plant species occurring from sea-level to 765 m a.s.l. on Marion Island (Huntlely, 1970; Frenot et al. 1993). It is widely distributed on the Macquarie, Crozet, Kerguelen, Heard, and Prince Edward Islands in the sub-Antarctic, where it plays a significant role in the vegetation of these islands (Huntley, 1972). Its tolerance to cold, harsh, and exposed environments is mainly attributed to its hard compact growth form. Water and heat loss are reduced through its tightly packed leaves and stems growing closely to each other (Huntley, 1972; Callaghan and Emanuelsson, 1985; Orchard, 1989).

Azorella selago is widespread across the island (Huntley, 1972; Smith et al., 2001), and also dominant on fellfield habitat (Huntely, 1972; Orchard, 1989; Frenot et al., 1993). The fact that this cushion occurs from sea-level to 765 m a.s.l. on Marion Island

(Huntlely, 1970; Frenot et al., 1993) makes it the vascular plant species with the largest altitudinal range on the island (Moore, 1968; Gremmen, 1981; Smith et al., 2001). *Azorella selago* occupies loose scoraceous slopes of volcanic rocks, recent lava flows and forelands of retreating glaciers (Huntley, 1970; Frenot et al., 1998), hence it is a pioneer species which contributes to succession on the Island (Frenot et al., 1998). Furthermore, this plant species forms terraces on fellfield landscapes, also adding significantly to soil accumulation on these landscapes, thus forming a strong relationship with these geomorphological processes (Selkirk, 1998; Boelhouwers et al., 2000a; Brancaleoni et al., 2003). Finally, *A. selago* hosts a diversity of epiphyte species (i.e. moss, liverwort, lichen and vascular plant species) (Huntley, 1972; Brancaleoni et al., 2003; le Roux, 2004) and microarthropod communities (i.e. Acari (mites) and Collembolla (springtails) species) (Barendse and Chown, 2001; Hugo et al., 2004). It is therefore regarded as a keystone plant species on Marion Island (sensu Begon et al., 1996). The Marion Island plant community growing epiphytically on *A. selago* includes as many as 17 non-vascular (the taxonomy of many remain incomplete), and at least another 16 vascular plant species (McGeoch et al. in press). Most of these species are facultatively epiphytic at low altitudes (le Roux, 2004). However, the grass, *Agrostis magellanica* is the dominant epiphyte growing on *A. selago* cushions (Huntley, 1972; Gremmen, 1981; le Roux, 2004). *Agrostis magellanica* prevalence on *A. selago* cushions occurs from sea-level to approximately 550 m a.s.l on Marion Island (le Roux, 2004).

Fellfield habitat is characterized by nutrient-poor, mineral soils with high rock cover (Smith et al., 2001; Gremmen and Smith, 2004). It forms in higher altitude areas strongly exposed to wind and low temperatures (Gremmen, 1981). This habitat is regarded to be the oldest of the habitats on the sub-Antarctic islands (Scott, 1985). As mentioned above, *A. selago* is the most dominant plant species in various plant communities, but is most well developed on fellfield habitats occurring in almost monoculture-like stands (with the exception of its epiphytes, bryophytes and other non-vascular species) (Frenot et al., 1993).

SAMPLING

Azorella selago was sampled in grey lava, mesic fellfield habitat on Marion Island. The study was conducted from April 2004 to April 2005 in the three study sites on the eastern side of the island, i.e. Skua Ridge, Tafelkop and Tafelberg (Table1).

Thirty, randomly selected, low-density *A. magellanica*, and 50 high-density *A. magellanica* covered *A. selago* cushion plants were selected for treatments at each site (80 in total plants, see later description of treatment assignment). Healthy plants, free of mouse burrows dug by alien invasive mouse species *Mus musculus* L. (Muridae) (Chown and Smith, 1993) were selected. Plants of moderate size were chosen (circumference ranged from 51 to 525 cm amongst all areas) to avoid extreme size effects. Every effort was made not to damage small plants because of the low recruitment rates of the species (le Roux and McGeoch, 2004). Small *A. selago* plants do not have significant *A. magellanica* numbers relative to moderate sized plants, and larger plants tend to have more dead tissue due to aging and heavy epiphyte covers. A study conducted by Alliende and Hoffman, (1985) on another cushion plant *Laretia acaulis* (also Apiaceae) suggested that larger cushions have more possibilities of being colonised by more epiphytes. To control for some of this unwanted variability, plants in the extreme size categories were excluded in this study. Plants within the selected size range were randomly selected and were at least three plants apart from each other to avoid pseudo-replication. Plants may be considered independent of each other because of the consistent absence of, or extremely weak, spatial autocorrelation in plant characteristics across patches (Hugo, 2006; Nyakatya, 2006).

The selected plants were marked with aluminium tags and short wooden marker poles. Position was determined by using a Garmin 12MAP GPS (Garmin International, Kansas City, USA). All plants were photographed with a digital camera (photograph taken from approximately 1.5m above each plant), with a scale and compass direction marker included in each photograph. This was done to calibrate the size and orientation of the plants.

Treatments

Eight, randomly assigned treatments were applied to 80 selected plants at each altitude site (i.e. one study site at each of these altitudes). Treatments were applied to cushions during autumn (April and early May 2004) and spring (September and October 2004). There were ten replicates of each treatment at all three altitude sites. Treatments included (i) control high- and (ii) low-density *A. magellanica* cushions, (iii) autumn weeded (AW), (iv) spring weeded (SW), (v) autumn mown (AM), (vi) spring mown (SM), (vii) procedural control weeded (PCW), and (viii) procedural control mown (PCM) cushions (Figure 1 - 4).

The weeding treatments (AW and SW) involved weeding of *A. magellanica* from ten *A. selago* cushions per altitude site (Figure 3 = AW, Figure 4 = SW). This was done by carefully pulling up *A. magellanica* from cushions, extracting the roots while minimising damage to the cushions. The weeded grass was taken back to the laboratory to be dried at 60°C for 48 hours, to determine grass biomass. The roots were separated from the stems and leaves to determine the above and below ground biomass, and this material was weighed with a microbalance (Metteler AE163). There may be an underestimation on below ground biomass because not all roots were extracted from the cushion plants (although every effort was made to do so without damaging the cushion plants). However, the level of underestimation will be the same between treatments. This treatment was used to examine the shading effect of epiphytic *A. magellanica* on cushion plants. A procedural control for weeding (PCW) treatment was applied to five cushions per season in each altitude site, i.e. five cushions in autumn, and 5 cushions in spring. This treatment involved inserting a 2 cm metal rod, ten times, into the northern half of the cushions to standardise treatment application at all three altitude sites. The purpose of this treatment was to simulate the action of weeding described above.

The mowing treatment (AM, and SM) was also applied to ten plants per altitude site (Figure 5 = AM, Figure 6 = SM). The grass was cut as close to the surface of the cushions as possible using a pair of scissors. The mown grass was dried at 60°C for 48 hours and weighed roots. However, only the above ground biomass was weighed for the mown plants, since the mowing procedure only involved cutting the above material,

without extracting the roots. This treatment was designed in such a way that it examines the shading effect of *A. magellanica* on cushions without the potential physical damage caused to cushions by extracting the roots of *A. magellanica* as in the weeding treatment. A procedural control treatment for mowing (PCM) was applied to five cushions per season in each altitude site, i.e. five cushions in autumn, and 5 cushions in spring. A pair of scissors was used, cutting close to the cushion surface, causing minor abrasions to the surface of the cushion. This treatment was applied to simulate the action of mowing.

Additional measurements

The temperature within *A. selago* cushions was measured by i-button (Thermochron DS19221G, Dallas Semi-Conductors, Texas, USA) data loggers for a period of 11 months for Skua Ridge (low site) and Tafelkop (mid site), and 10 months for Tafelberg (high site). I-buttons were set to measure temperature (°C) at two hour intervals, then inserted 1-2 cm into the cushion with a tag sticking up out of the cushion. Insertion was performed on 5 of the cushions selected with low *A. magellanica* density, 5 of the selected cushions densely covered with *A. magellanica,* as well as to 5 weeded and 5 mown cushions. Insertion took place in May, followed by removal in September 2004 to download temperature measurements. I-buttons were reinserted into the same cushions in October 2004 and removed in March 2005. Cushion vitality was determined by rating each cushion on a scale of 1 – 10 (1-3 = very weak, 4-6 = clearly reduced but still largely healthy, 7-8 = above average health, 9-10 = healthy plant with no sign of stem die-back or decay) (following Huntley, 1972). These vitality scores were determined from all selected cushions before treatment application. However, cushion vitality was only determined for low altitude cushions due to weather constraints. Phenological variables were measured for *A. selago* every month. At low and middle altitude sites, phenology was monitored from August 2004 to February 2005, and at the highest altitude from October 2004 to February 2005. Weather conditions at high altitudes were relatively colder with cushions still covered with some snow, hence measuring phenological

variables only commenced in October. For plants with high grass cover, phenological variables were estimated for the cushion surface area not covered by grass.

Analysis

To test for altitude site treatment effects on *A. selago* microclimate temperature, General Linear Models (GLMs) (Stat Soft, Inc. 1984 – 2003) were used. The model was constructed in such a way that temperature measures were categorised separately according to different months, representing different seasons (July = winter, September = spring, December = summer, and March = autumn), with altitude site and treatment as the independent variables. The results are presented as tables and box plots.

A Nonparametric, Kruskal-Wallis Analysis of variance test (Stat Soft, Inc. 1984 – 2003) was used to examine the effect of epiphytic *A. magellanica* on *A. selago* vitality. The same test was also used to examine the effect of altitude site on epiphytic *A. magellanica* biomass. The results are presented as box plots.

To test for the effect of treatments from three altitude sites, at different seasons (October = spring, December = summer, and March = autumn) on *A. selago* cushion phenology, General Linear Models (GLMs) (Stat Soft, Inc. 1984 – 2003) were used. Square-root Arcsine transformations were used to achieve normal distributions for (some) phenological traits. Each phenological trait (% green, % brown, % budding, and % flowering plant surface area) was used in the model as a dependent variable with altitude, treatment and month as independent variables. Different models were constructed separately for weeded and mown treatments. The results are presented as a table and box plots.

Results

TEMPERATURE

Temperature associated with *A. selago* at three altitude sites on the island showed a significant difference between altitudes for all four seasons (Table 2), particularly in July (mid-winter), and warmest areas across all sites in December (mid-summer). Temperature at the high altitude site was cooler than mid and low site (Table 3). The mid altitude site was not always significantly cooler than the low site (Table 3, Appendix A, Appendix B). The low altitude site was on average between 2.61 and 0.5°C warmer than the high altitude site (winter = 1.44°C, spring = 2.61°C, summer = 0.5°C, autumn = 2.07°C) (Table 3). Also, the mid altitude site was on average between 1.91 and 0.43 °C warmer than high altitude site (winter = 1.24°C, spring = 1.34°C, summer = 0.43°C, autumn = 1.91°C) (Table 3). The low altitude site was on average between 1.27 and 0.07°C warmer than the mid altitude site (winter = 0.2°C, spring = 1.27°C, summer = 0.07°C, autumn = 0.16°C) (Table 3). There was no significant difference in *A. selago* temperature after treatment application for all the seasons (Table 2, Figure 4). The greatest differences in temperature between the three altitude sites were in spring and autumn. The treatments applied to cushions did therefore not affect cushion temperature.

VITALITY

There was a significant difference in cushion vitality between low and high grass density cushions ($H_1 = 8.12$, N = 80, p = 0.004) (Figure 5). Vitality of plants with high epiphyte cover was lower than plants with low epiphyte cover (Figure 5). This is illustrated using two cushions as an example in Figure (6a, b). The low vitality cushion was a high grass cushion prior to treatment, and the picture shown here is after the application of weeding (Figure 6b). Figure 1a is an untreated, high vitality cushion for comparison.

GRASS BIOMASS

There was no significant difference in weeded *A. magellanica* above ground biomass between the three altitude sites in autumn (H_2 = 4.64, N = 30, p = 0.09) (Figure 7a). There was a significant difference in weeded *A. magellanica* below ground biomass between the three altitude sites in autumn (H_2 = 6.43, N = 30, p = 0.04) (Figure 7b). However, multiple comparison tests were not significant (Figure 7b). Weeded *A. magellanica* above and below ground biomass showed a significant difference between the three sites in spring (above = H_2 = 8.24, N = 30, $p < 0.05$, below = H_2 = 10.4, N = 30, $p < 0.01$) (Figure 7c, d). For grass weeded in spring, the low altitude site had a higher above ground biomass than at the high altitude site (Figure 7c). Below ground biomass of grass weeded in spring was also high at the low altitude site than at the mid and high altitude sites (Figure 7d). There was a significant difference in above ground biomass of grass mown in autumn between the three altitude sites (H_2 = 7.93, N = 30, $p < 0.01$) (Figure 7e). The mid altitude site had more grass biomass than the high altitude site (Figure 7e). There was no significant difference in above ground biomass of grass mown in spring between the three altitude sites (H_2 = 4.3, N = 30, p = 0.11) (Figure 7f). There was therefore a general tendency for epiphyte grass biomass per unit cushion area to be higher at the low and high altitude site, although this was not always significant.

VEGETATIVE AND REPRODUCTIVE PERFOMANCE

Comparison of weeded and mown plants at each across altitude site

There was a significant difference in *A. selago* percentage green surface area between three altitude sites for both weeded and mown treatments in models including site, treatment and month as factors (Table 4, Figure 8a, b). The vegetative and reproductive structures of weeded and mown plants were found to be extremely similar and they are considered together here (Table 4). The low altitude site cushions were significantly more green, with a declining percentage with altitude (Figure 8a, b). Brown percentage surface

area, as expected, showed the opposite pattern, with a significant increase of brown percentage surface area with altitude (Table 4, Figure 9a, b). High altitude site cushions had more brown plant cover than both mid and low altitude site cushions (Figure 9a, b). Budding and flowering both occurred between November and March. There was no significant difference in budding between altitude sites (Table 4, Figure 10a, b). The percentage of flowering showed a different trend, with a significant difference between altitude sites (Table 4) (Figure 11a, b). The percentage of plant surface area covered by flowers for weeded plants was different between all three altitudes, with a large percentage plant cover of flowers at the high altitude site (Figure 11a). However, mown plants produced a large percentage cover of flowers at the high and mid altitude sites relative to the low altitude site cushions (Figure 11b).

Comparison between treatments in weeded plants

There was no significant difference in percentage green surface area between treatments (Table 4, Figure 12a). Again, the weeded and mown treatments showed similar differences across treatments. The percentage of brown surface area showed a significant difference between treatments (Table 4). Cushions weeded in autumn and spring both had a high percentage of brown surface area than high, low and procedural control plants (Figure 13a, Appendix C). There was a significant difference in percentage of budding surface area between treatments (Table 4). Low grass density cushions produced a higher percentage surface area of buds than high grass density, autumn weeded, and spring weeded cushions (Figure 14a, Appendix C). Also cushions weeded in autumn produced a higher percentage of buds than procedural control weeded plants (Figure 14a, Appendix C). There was a significant difference in percentage of flowering surface area between treatments (Table 4). Low grass density cushions and procedural control weeded cushions produced the highest percentage surface area of flowers as compared to spring and autumn weeded, and high grass density plants (Figure 15a, Appendix C).

Comparison between treatments in mown plants

There was no significant difference in percentage green surface area between treatments (Table 4, Figure 12b). The percentage surface area of brown showed a significant difference between treatments (Table 4). However, a multiple comparison test did not show a clear significant difference between treatments (Figure 13b). There was a significant difference in percentage budding surface area between treatments (Table 4). Cushions with low grass density had a high budding plant cover relative to high grass density and autumn mown plants (Figure 14b, Appendix C). Flowering also followed the same trend as budding, where there was a significant difference in percentage cover of flowering between treatments (Table 4). Low grass density cushions had a high percentage surface area of flowers compared to high grass density, autumn mown, and spring mown plants (Figure 15b, Appendix C).

COMPARISON OF THE TIMING OF REPRODUCTIVE STRUCTRES

Weeded plants

The percentage of green surface area on cushions increased until plants started budding in November (Figure 16a, b, c, Appendix D - K) for all treatments. However, the percentage of brown surface area expectedly decreased until the period of budding (Figure 17a, b, c, Appendix D - K). For weeded plants flower buds occurred during November and December for all treatments at the low and high altitude sites with a higher percentage of flower buds for procedural control weeded plants at the low and high altitude sites (Figure 18a). The mid altitude site had a great percentage of flower buds for high grass abundance cushions, with flower buds emerging in October (Figure 18b). The high altitude site showed a similar trend to the low altitude site, with flower buds emerging during November and December for all treatments, and a higher percentage of flower buds for procedural control weeded plants at the low and high altitude sites (Figure 18c). The majority of flowers on cushions appeared between January and March at both low

and mid altitude sites and December to March at the high altitude site (Figure 19a, b, c). At the low and high altitude sites, procedural control weeded plants produced a large percentage cover of flowers than the other treatments, however, a large percentage cover flowers was produced by low grass density plants at the mid altitude site (Figure 19a, b, c). The period of flowering therefore increased with altitude; with a longer period and most flowers at the high and mid altitude sites when compared to the low altitude site (Figure 19a, b, c).

Mown plants

The percentage of green surface area on cushions for the mown treatment followed a similar trend as the weeded treatment. The percentage of green surface area on cushions increased until the budding period started in November for all treatments (Figure 20a, b, c, Appendix D – K). The percentage of brown surface area also decreased until the budding period started (Figure 21a, b, c, Appendix D – K). Flower buds emerged in November and December for all treatments at the low and high altitude sites with a higher percentage of flower buds for procedural control weeded plants at the low and high altitude sites (Figure 22a). However, the mid altitude site had a larger percentage of flower buds for low grass abundance cushions, with flower buds emerging in October (Figure 22b). The high altitude site showed a similar trend to the low altitude site, with flower buds emerging during November and December for all treatments, and a higher percentage of flower buds for procedural control weeded plants at the low and high altitude sites (Figure 22c). The majority of flowers on cushions appeared between January and February at the low altitude, January to March at mid, and December to March at the high altitude site (Figure 23a, b, c). The low altitude site produced cushions with a great flowering percentage for low and high grass abundance cushions than the rest of the treatments (Figure 23a). Low grass abundance cushions at the mid altitude site produced a great percentage of flowering cushion area when compared to other treatments (Figure 23b). High altitude site spring mown cushions produced more flowers per surface area than the rest of the treatments (Figure 23c). The period of flowering

therefore was highest at the high altitude site; with a longer period and most flowers at the high site when compared to the mid and low altitude sites (Figure 23c).

Discussion

Effects of shading

Azorella selago microclimate temperature showed no significant difference between treatments. A previous study on Marion Island also reported no difference in temperature and moisture content associated with *A. magellanica* (Hugo et al., 2004). This suggests surprisingly that epiphytic *A. magellanica* cover has little effect on microclimate temperature in *A. selago* plants. One would expect epiphytes to increase temperature because they buffer cushion surface from wind. However, epiphytes also shade the cushion surface from direct solar radiation and this is likely to keep the cushion cooler than it would have been if it was exposed to solar radiation. A previous study on tropical epiphytes suggested that epiphytes have a cooling effect on host plants (Freiberg, 2001). The non-significant temperature difference could therefore be attributed to the fact that temperature difference might not be shown through monthly averages but may be distinct when measuring daily temperature fluctuations.

Agrostis magellanica epiphyte cover had an effect on *A. selago* characteristics. Cushions weeded in autumn and spring had significantly more brown percentage surface area compared to high and low grass, and procedural control weeded plants. This pattern shows that weeded cushions may be taking a longer period to recover from the damage caused by the colonisation of *A. magellanica*, as well as the disturbance caused by the action of weeding. However, simulating the action of weeding (PCW) had no effect on cushions, since the percentage surface area of brown was most similar to that of low grass covered cushions. The small percentage of brown surface area for high grass cushions when compared to the weeded treatments may be due to an underestimation, since only the exposed part of the cushions could be clearly measured, whereas the whole cushion was measured for the other treatments. This means that not only is cushion surface area

(leaves) under the epiphyte brown, but these stems do not recover rapidly after removal of the epiphyte, *A. magellanica*. The fact that *A. selago* leaves under the epiphytes remain brown shows that *A. magellanica* reduces the photosynthetic surface area of *A. selago.*

There was also a significant difference in *A. selago* budding percentage surface area between treatments. Low grass density cushions produced more flower buds than high grass density cushions. This suggests that epiphytic *A. magellanica* reduces the reproductive surface area of cushions, or at least the number of flowers produced per cushion, and this reduces the reproductive potential of individual plants. Plants that are exposed to less sunlight and lower temperatures would be expected to produce fewer flowers due to a decreased photosynthetic surface area and thus decreased photosynthetic rates (Callaghan et al., 1992). Low grass density and procedural control weeded cushions produced almost the same percentage of flower buds, suggesting that simulating the action of weeding did not impose any damage to the plants. The low percentage cover of flower buds in cushions weeded in autumn and spring shows that the plants do not recover rapidly from the damage caused by epiphytic *A. magellanica* after its removal (at least not within 4 months at the low and mid altitude-areas, and 5 months at the high altitude-area for the cushions weeded in autumn; and one month for the cushions weeded in spring). The percentage cover of flowers followed a similar trend as flower budding. A similar trend was observed for mown cushions for almost all vegetative and reproductive structures, suggesting a similar response of cushions to shading.

Cushion vitality also showed an apparent difference between low and high cover *A. magellanica* cushions, with relatively high vitality score on low grass density cushions compared to high grass density cushions. Vitality shows the health of a cushion, where scores are assigned to cushions accordingly. Some cushions tend to have dead parts, especially on parts of the cushions highly colonised by epiphytic *A. magellanica*. The low grass density cushions were healthy, with no sign of die-back or decay. Further colonization on *A. selago* cushions by epiphytic *A. magellanica* is therefore likely to impose negative effects on cushions by a decrease in the photosynthetic surface area of plants, a decrease in flower buds and flowering surface area of *A. selago* cushions, as well as decrease in vitality.

Between altitude site differences in micro-temperature and treatment effects

The microclimate temperature associated with *A. selago* was highest for low altitude site cushions, declining significantly at the high altitude site, as expected (Chapter 2). Microhabitat temperatures are significantly related to wind speed and solar radiation (Chown and Crafford, 1992), and since lower altitudes experience a milder wind speed and higher solar radiation, higher temperatures would be expected at the low altitude site (Blake, 1996).

Low altitude cushions had significantly more green surface area and this declined with altitude. This suggests that growth begins earlier at the lower altitude than at the high altitude site (Chapter 2). The percentage of flowering surface area was significantly different between the three altitude sites. There was an apparent difference between all three altitudes, with the high altitude plants producing the most flowers, intermediate at mid altitude, and the least at the low altitude site. The low percentage of flowering surface area on cushions at the low altitude site is coupled with a decreased flowering period, which begins earlier and is rapid at this warmer altitude site. The flowering period at the low altitudes lasts for 2 months, however cushions at the high altitude flower for a period of 3 months. Similar results were reported on a previous study from Marion Island, where the flowering stage of *A. selago* was shorter at the warmer, lower altitudes with earlier autumnal senescence (Nyakatya, 2006; Chapter 2). This agrees with the fact that temperature and photoperiod play an important role in acting as environmental stimulus for flowering (Evans, 1971). The length and extent of flowers could therefore be influenced by both altitude temperature differences between altitude sites as shown on the previous chapter. The previous chapter also shows that the number of *A. magellanica* growing off *A. selago* cushions declines much rapidly than *A. magellanica* on cushions, suggesting a facilitation effect at higher altitude sites by *A. selago* cushions. However, this facilitative interaction could have negative affects on *A. selago*, since heavy epiphyte numbers apparently impose negative effects on cushion phenology and vitality. Previous studies also predict that under further warming and milder winds, *A. magellanica* may colonise upslope cushions (le Roux, 2004), increasing the proportion of individuals of the *A. selago* population on the island negatively impacted by this epiphyte.

Agrostis magellanica above ground biomass weeded in spring showed an apparent association with altitude site. The above and below grass biomass was greater at the low altitude than at the high altitude site. However, previous experimental warming studies in alpine tundra environments report little effect of warming on total above ground biomass (Havstrom et al., 1993; Wookey et al., 1993, 1994; Parson et al., 1994; Harte and Shaw, 1995; Parson et al., 1995; Chapin and Shaver, 1996; Michelson et al., 1996; Hobbie and Chapin, 1998). Plant biomass accumulation is affected by both temperature and nutrient availability, rather than temperature alone and will only increase if organic nutrients are also stimulated (Hobbie and Chapin, 1998). In the longer term, increased air temperatures are predicted to cause increased substrate temperatures, thus leading to increased decomposition rates (Shaver et al., 1992). The greater above ground grass biomass at the warmer, low altitude site could therefore be attributed to both higher temperatures and more nutrients inside *A. selago* cushions. Previous studies report possible provision of organic substrates to plants intruding cushions (Griggs, 1956; Alliende and Hoffman, 1985). The nutrient rich *A. selago* could therefore have a more positive effect on above ground grass biomass with further warming up on the island.

The effect of treatments on *A selago,* together with the direction of *A. magellanica* growing on and off *A. selago* cushions suggests that the vegetative and reproductive performance of *A. selago* and cushion vitality are likely to be negatively affected under climate change on Marion Island. The nature of the relationship between *A. selago* and *A. magellanica* shows that *A. magellanica* competes with *A. selago,* whereas *A. selago* facilitates *A. magellanica.* This therefore suggests an asymmetric association since a positive association is only shown in one direction. Asymmetric competition results in one species gaining more fitness at the expense of the other by using a disproportional large amount of resources (Freckleton and Watkinson, 2001). Further changes in climate could therefore have an indirect negative effect on *A. selago*. Hence ongoing monitoring of this keystone species and the interaction with its dominant epiphyte, *A. magellanica* is critical, including monitoring the altitude range of *A. magellanica* on the island to detect early signs of a possible upslope expansion in the altitudinal range of this species on Marion Island.

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TABLE 1

General description for the three study sites.

Information	Skua Ridge (Low)	Tafelkop (Mid)	Tafelberg (High)
Altitude (m. a. s. l)	103	176	375
Lava type	Grey	Grey	Grey
Slope	Moderate	Gentle	Gentle
GPS position at centre of area	46°51`S, 37°50`E	46°52`S, 37°49`E	46°53`S, 37°47`E

TABLE 2

Differences in Azorella selago *temperature between sites at three altitudes, treatments and altitude*treatment in four different seasons. All statistics are derived from General Linear Models described in the text (based on an Analysis of Variance).*

Overall model results		Independent factors					
		Altitude site		Treatment		Altitude*Treatment	
F (d. f.)	p	F(d. f)	p	F(d. f)	p	F(d. f)	p
July (Winter)							
4.66 (11, 36)	<0.001	19.76 (2, 36)	<0.001	2.27 (3, 36)	0.09	0.83 (6, 36)	0.55
September (Spring)							
19.22 (11, 36)	<0.001	103.08 (2, 36)	<0.001	0.14 (3, 36)	0.90	0.82 (6, 36)	0.55
December (Summer)							
2.14 (11, 36)	0.040	8.12 (2, 36)	0.001	1.89 (3, 36)	0.14	0.28 (6, 36)	0.94
March (Autumn)							
30.36 (11, 36)	<0.001	163.84 (2, 36)	<0.001	1.30 (3, 36)	0.28	0.40 (6, 36)	0.87

TABLE 3

Temperature inside A. selago *cushions in four different seasons (means and standard errors for General Linear Models examining the effect of area and treatment on plant temperature), n = 16 cushions. Means with different letters in superscript are significantly different at p < 0.05 (based on an Analysis of Variance). Means are presented from the largest to smallest as is convention for multiple contrasts.*

Month	Altitude site	Mean ± s. e
July		
(Winter)	Low	2.95 ± 0.17^{a}
	Middle	2.75 ± 0.17^{a}
	High	1.51 ± 0.17^{b}
September		
(Spring)	Low	4.69 ± 0.12^{a}
	Middle	3.42 ± 0.12^{b}
	High	2.08 ± 0.12^{c}
December		
(Summer)	Low	9.02 ± 0.09^{a}
	Middle	8.95 ± 0.09^{a}
	High	8.52 ± 0.09^{b}
March		
(Autumn)	Low	9.55 ± 0.09^{a}
	Middle	9.39 ± 0.09^{a}
	High	7.48 ± 0.09^{b}

TABLE 4

Differences in A. selago *phenological traits (i.e median % green, % brown, % flower buds, % flowering plant surface area) between sites, treatments, and for three different seasons (October, December and March). All statistics are derived from General Linear Models described in text (based on an Analysis of Variance). Means are presented from the largest to smallest as is convention for multiple contrasts.*

		Independent factors					
Overall model results		Altitude site		Treatment		Month	
F (d. f.)	p	F(d. f)	p	F(d. f)	p	F(d. f)	p
Weeded							
% Green							
22.23 (8, 441)	<0.001	45.38 (2, 441)	<0.001	2.37 (4, 441)	0.050	38.66 (2, 441)	<0.001
% Brown							
38.37 (8, 441)	<0.001	22.44 (2, 441)	<0.001	10.53 (4, 441)	<0.001	83.91 (2, 441)	<0.001
% Flower buds							
69.79 (8, 441)	<0.001	1.19 (2, 441)	0.300	6.47 (4, 441)	<0.001	265.03 (2, 441)	<0.001
% Flowering							
32.16 (8, 441)	<0.001	30.78 (2, 441)	<0.001	7.07 (4, 441)	<0.001	83.91 (2, 441)	<0.001
Mown							
% Green							
19.54 (8, 441)	<0.001	37.54 (2, 441)	<0.001	1.68 (4, 441)	0.150	37.28 (2, 441)	<0.001
% Brown							
32.94 (8, 441)	<0.001	22.75 (2, 441)	<0.001	2.50 (4, 441)	0.040	104.02 (2, 441)	<0.001
% Flower buds							
53.11 (8, 441)	<0.001	1.51 (2, 441)	0.21	2.99 (4, 441)	0.010	204.94 (2, 441)	<0.001
% Flowering							
28.66 (8, 441)	<0.001	26.88 (2, 441)	<0.001	4.43 (4, 441)	0.001	78.89 (2, 441)	<0.001

TABLE 5

Difference in A. selago *phenology i.e. % brown, % flower buds, % flowering surface area between seasons (October, December, and March), (means and standard errors for the GLM model examining the effect of season on phenology). All percentages were transformed using square root arcsine, n = 150. Means with different letters in superscript are significantly different at $p < 0.05$ (based on an Analysis of Variance). (See table 4). Means are presented from the largest to smallest as is convention for multiple contrasts.*

Phenlogical traits	Month	mean ± s. e
Weeded		
%Green	March	1.090 ± 0.008^{a}
	December	1.020 ± 0.008^{b}
	October	0.990 ± 0.008^{c}
%Brown	October	0.510 ± 0.008^{a}
	March	0.410 ± 0.008^{b}
	December	0.330 ± 0.008^{c}
%Budding	December	0.350 ± 0.010^{a}
	October	0.090 ± 0.010^{b}
%Flowering	March	0.120 ± 0.007^{a}
	December	0.020 ± 0.007^{b}
Mown		
%Green	October	1.090 ± 0.007^{a}
	December	1.010 ± 0.007^{a}
	March	1.002 ± 0.007^{b}
%Brown	October	0.520 ± 0.008^{a}
	March	0.420 ± 0.008^{b}
	December	0.350 ± 0.008^{c}
%Budding	December	0.350 ± 0.010^{a}
	October	0.070 ± 0.010^{b}
	March	0.0003 ± 0.01^{c}
%Flowering	March	0.120 ± 0.007^{a}
	December	0.020 ± 0.007^{b}
	October	0.0003 ± 0.007^{b}

a)

b)

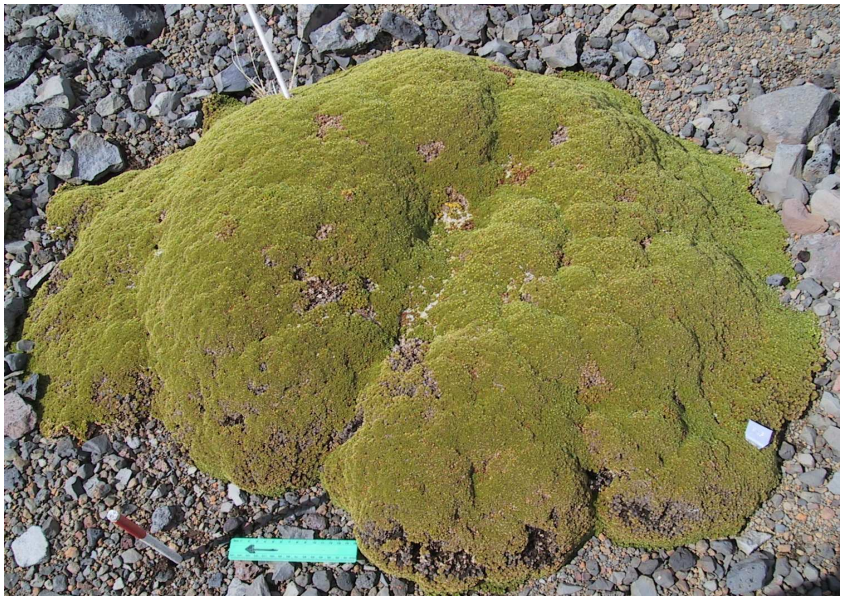


FIGURE 1. Examples of cushion plants with high (a) and low (b) A. magellanica *cover. The ruler represents the scale (15 cm) as well as direction (arrow pointed to the north). Pictures for cushions were taken in November 2005.*

a)

b)

FIGURE 2. Examples of cushion plants that underwent weeding in autumn (a), and weeding in spring (b). The ruler represents the scale(15 cm) as well as direction (arrow pointed to the north). Picture for cushion a) was taken 5 months after treatment application (October 2004), b) immediately after treatment application (October 2004).

a)

b)

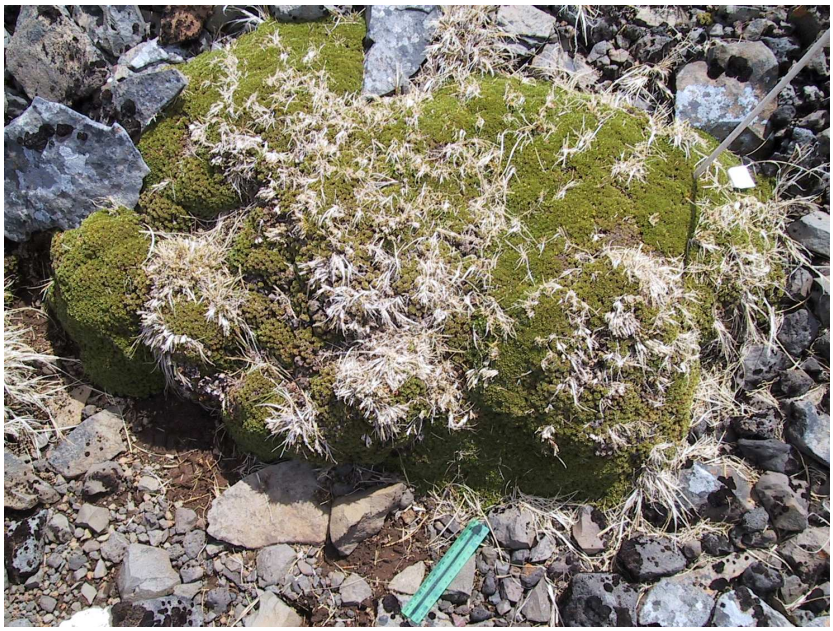


FIGURE 3. Examples of cushion plants that underwent mowing in autumn (a), and mowing in spring (b). The ruler represents the scale (15 cm) as well as direction (arrow pointed to the north). Picture for cushion a) was taken 5 months after treatment application (October 2004), b) immediately after treatment application (October 2004).

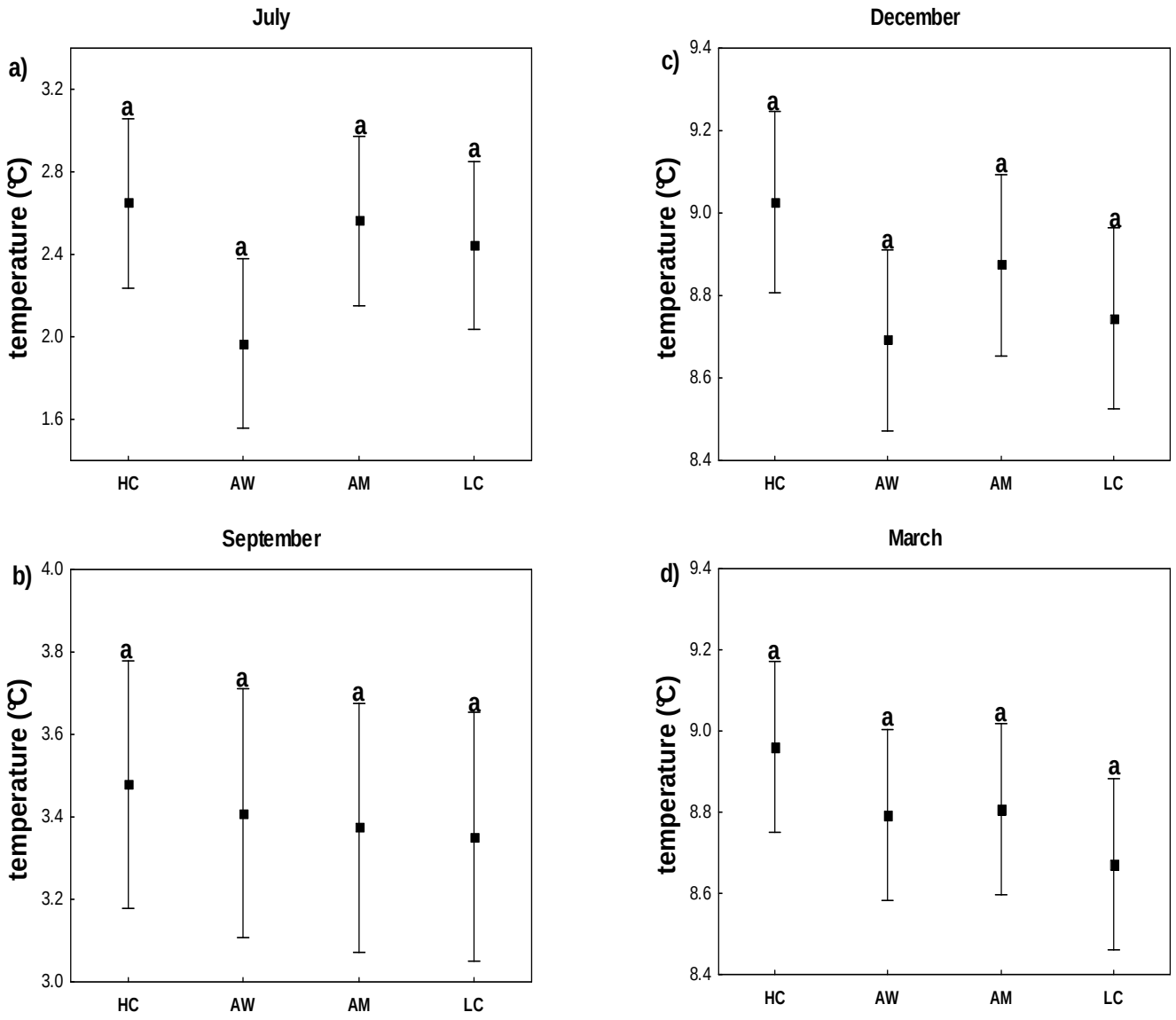


FIGURE 4. Mean temperatures inside A. selago *(mean ± 95% Confidence Interval) between treatments (HC = high grass density plants, AW = plants weeded in autumn, AM = plants mown in autumn, LC = low grass density plants) for the three given month. Means with same letters are not significantly different at $p < 0.05$ (based on an Analysis of Variance).*

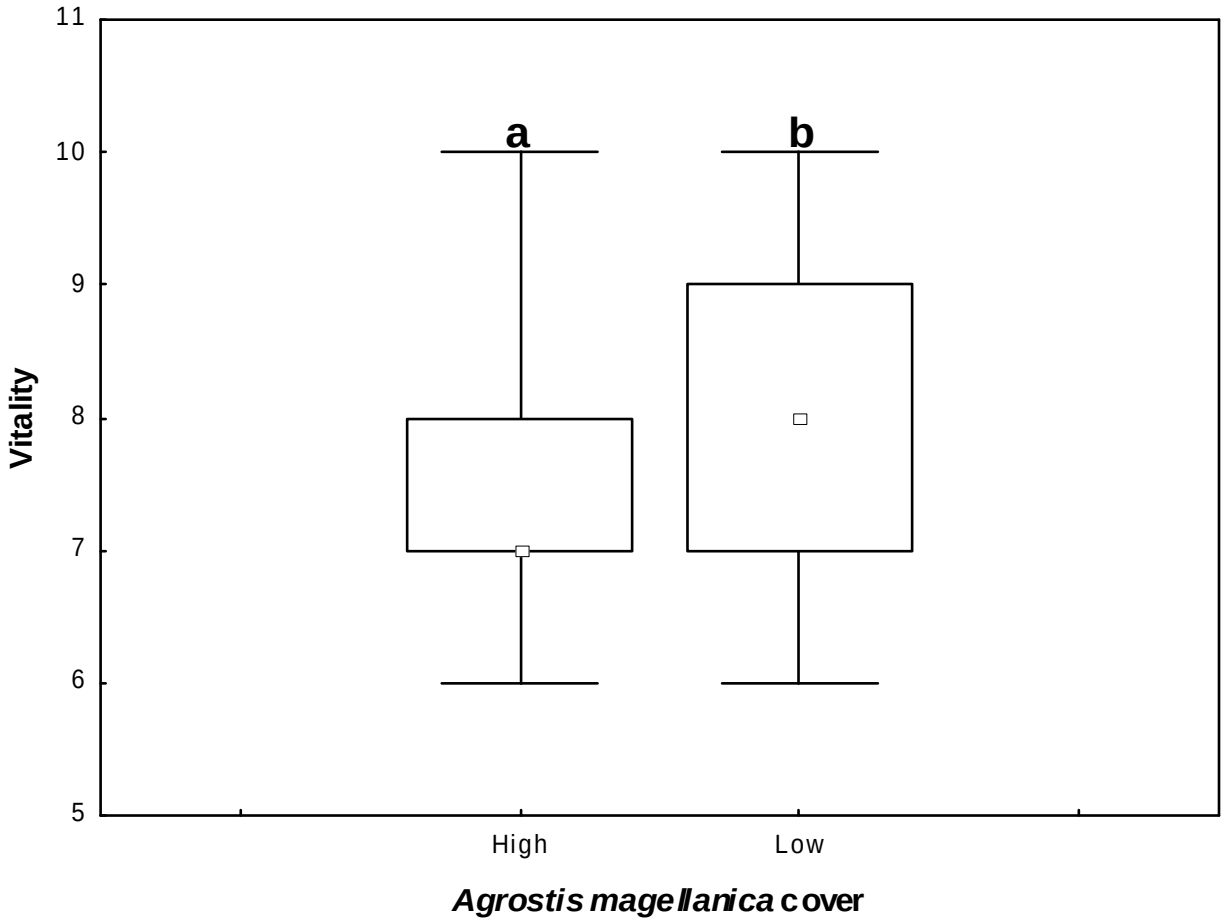
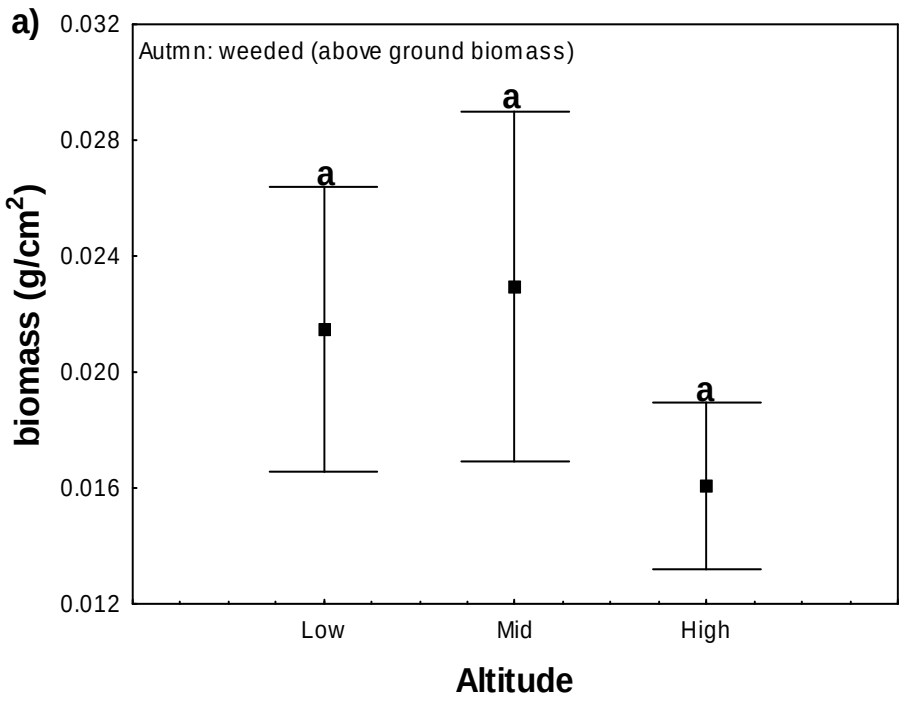


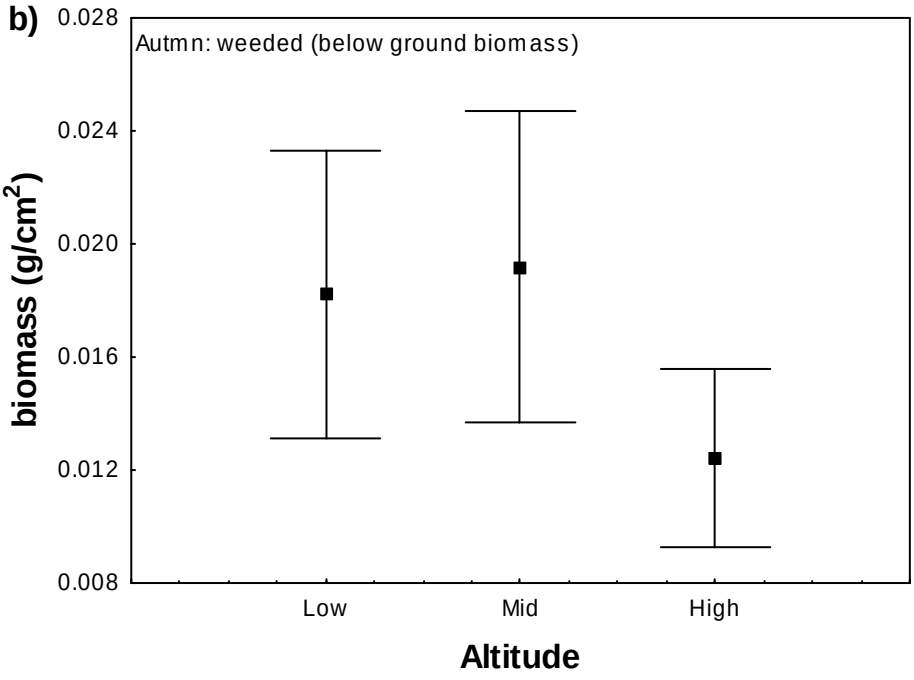
FIGURE 5. Qualitative estimation of A. selago *vitality at the low altitude site between cushions with low and high* A. magellanica *cover. Medians with different letters are significantly different at p < 0.05. Median, 25 - 75% quartiles, range. Vitality ranking between 1 (low vitality) – 10 (high vitality) (based on an Analysis of Variance).*

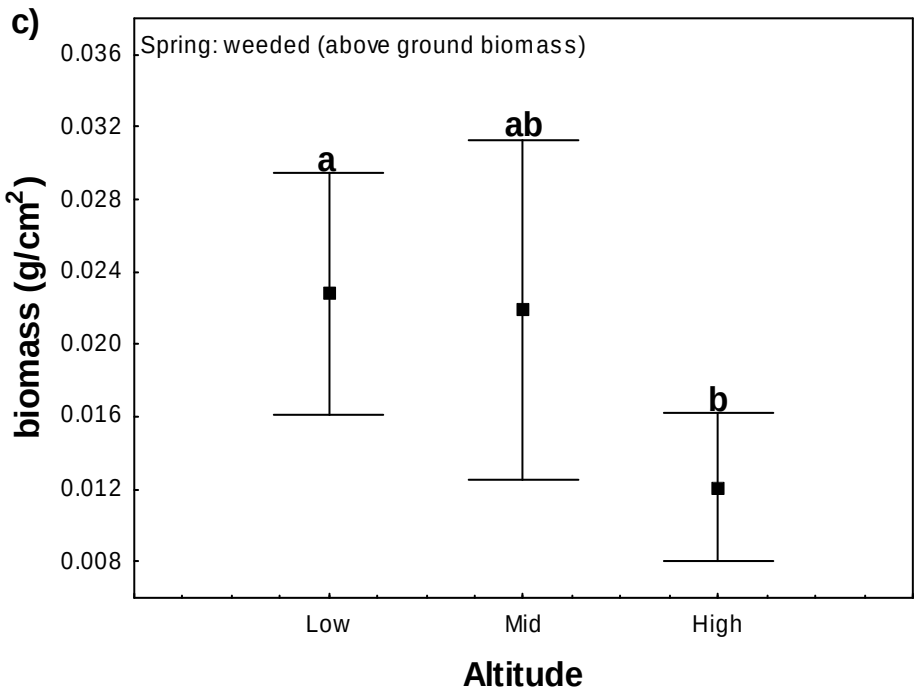
a)

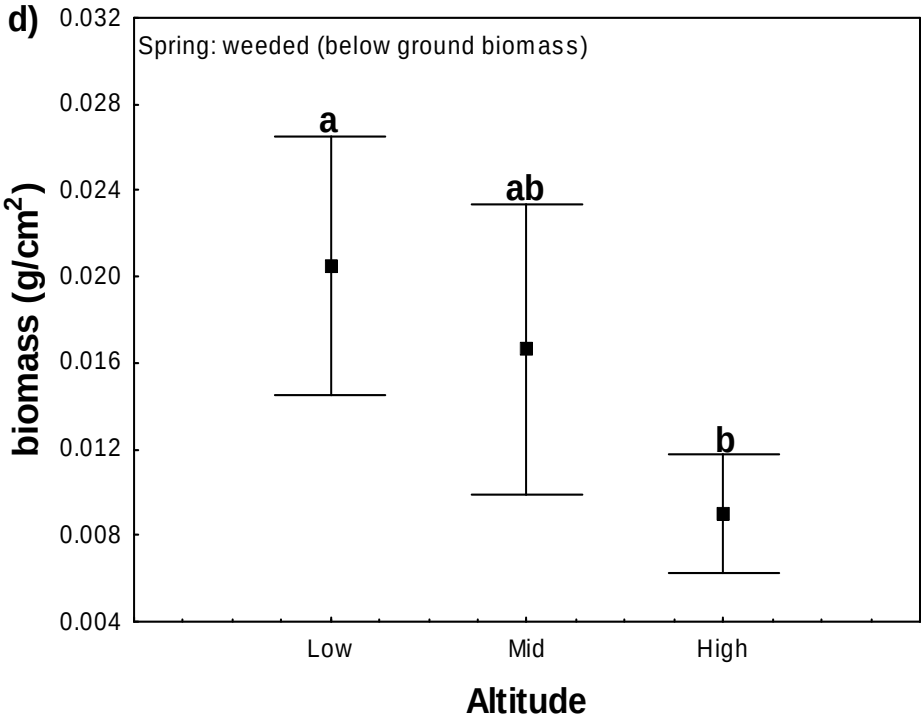
b)

FIGURE 6. Examples of A. selago *cushions showing a) high and b)low vitality.*


a)
Autmn: weeded (above ground biomass)
biomass (g/cm2)
0.032
0.028
0.024
0.020
0.016
0.012
a
a
a
Low
Mid
High
Altitude


b)
Autmn: weeded (below ground biomass)
biomass (g/cm2)
0.028
0.024
0.020
0.016
0.012
0.008
Low
Mid
High
Altitude


c)
Spring: weeded (above ground biomass)
0.036
0.032
0.028
0.024
0.020
0.016
0.012
0.008
biomass (g/cm2)
a
ab
b
Low
Mid
High
Altitude


d)
Spring: weeded (below ground biomass)
0.032
0.028
0.024
0.020
0.016
0.012
0.008
0.004
biomass (g/cm2)
a
ab
b
Low
Mid
High
Altitude

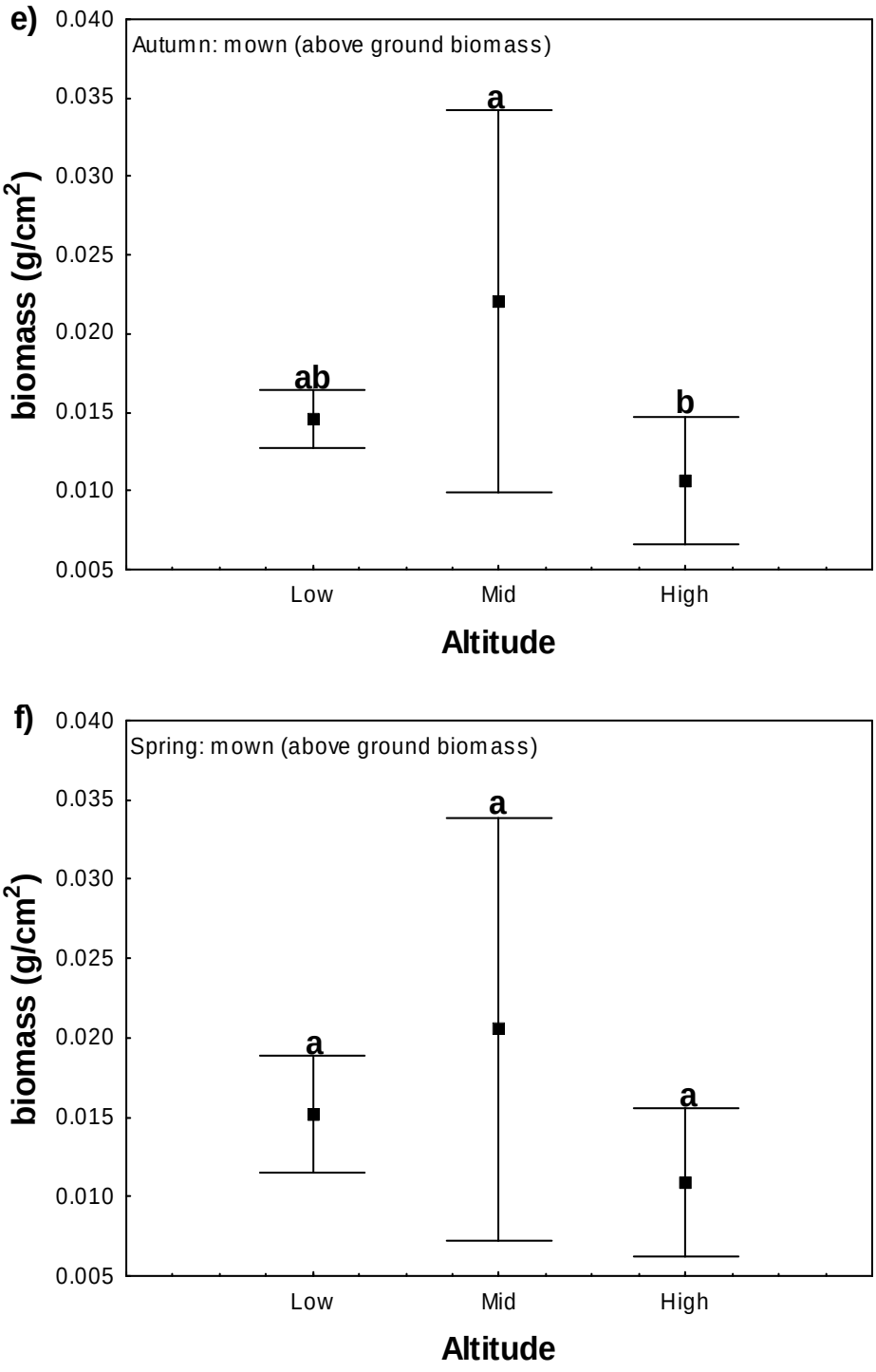


FIGURE 7. Mean biomass of A. magellanica *(mean ± 95% Confidence Intervals) per cushion plant for weeded and mown* A. magellanica *at the three sites (n = 10 cushions). Means with different letters are significantly different at p < 0.05 (letters not shown on b because multiple comparison test results were not significant) (based on an Analysis of Variance).*

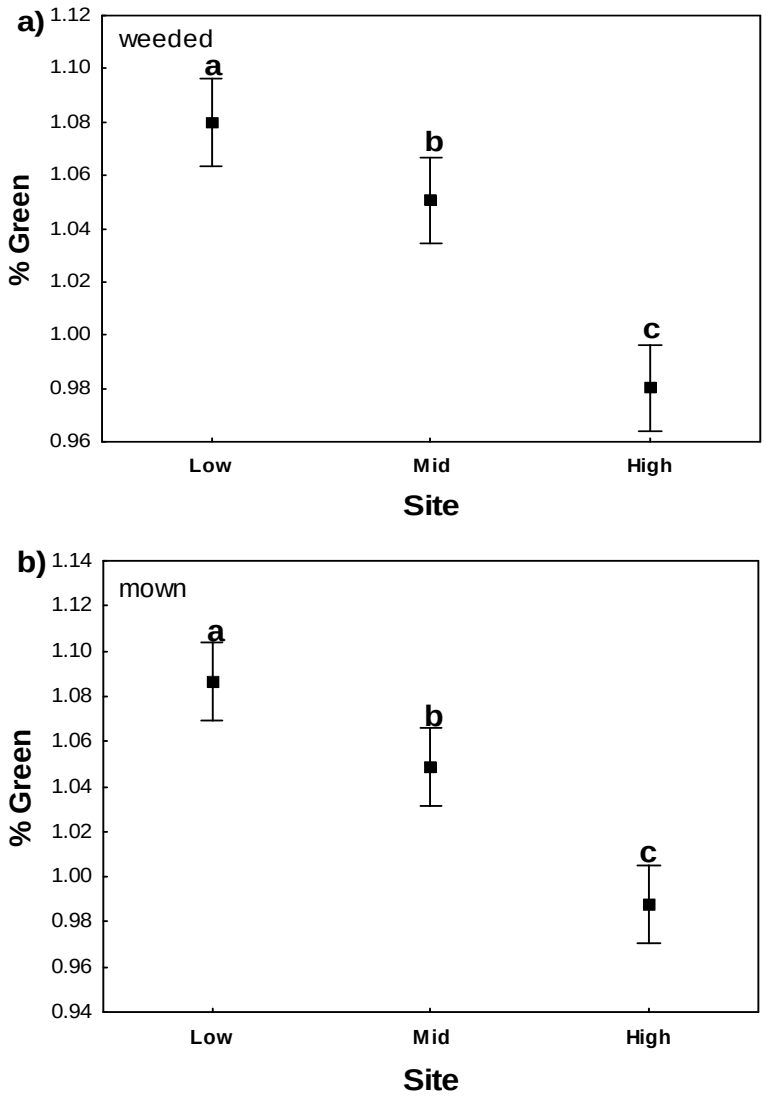


FIGURE 8. Means and 95% Confidence Intervals for General Linear Models examining the effect of altitude site on A. selago *% green surface area at three altitude sites (i. e. low, mid, high), (a) weeded, (b) mown plants. Means with different letters are significantly different at $p < 0.05$ (based on an Analysis of Variance). (Means are predicted means for General Linear Models, holding treatment and month constant).*

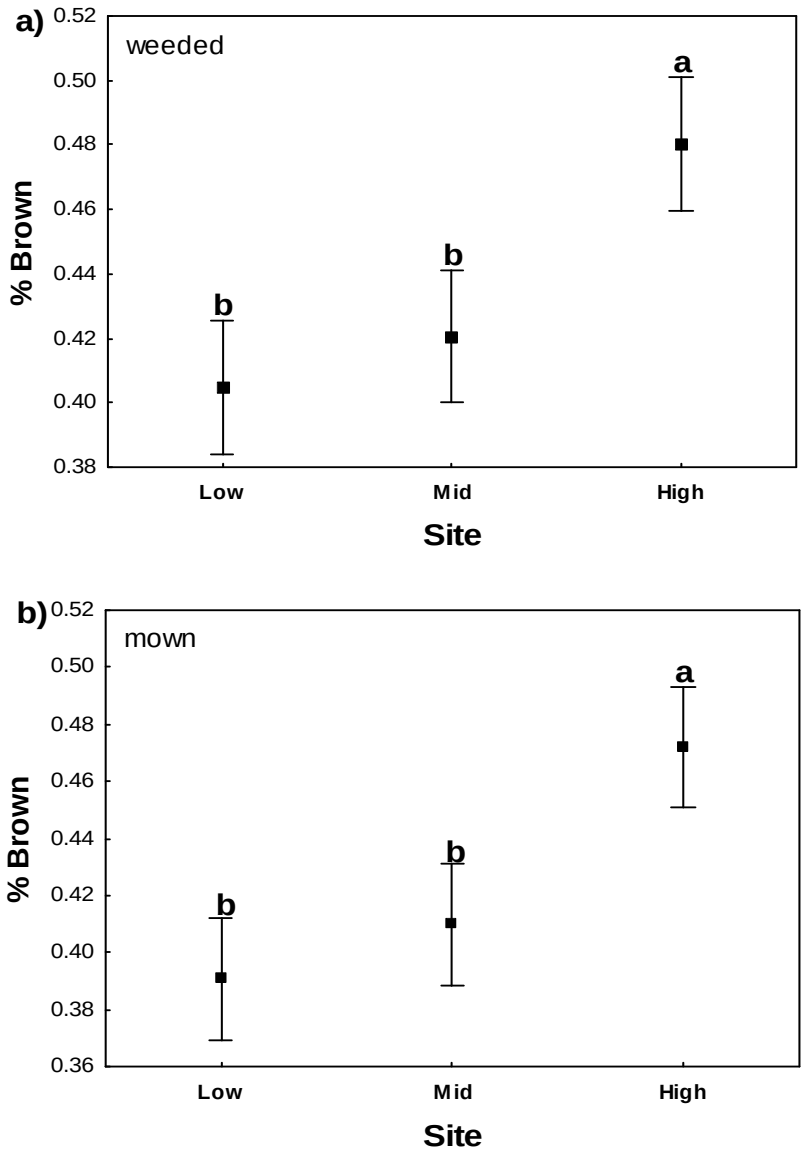


FIGURE 9. Means and 95% Confidence Intervals for General Linear Models examining the effect of altitude site on A. selago *% brown surface area at three altitude sites (i. e. low, mid, high), (a) weeded, (b) mown plants. Means with different letters are significantly different at $p < 0.05$ (based on an Analysis of Variance). (Means are predicted means for General Linear Models, holding treatment and month constant).*

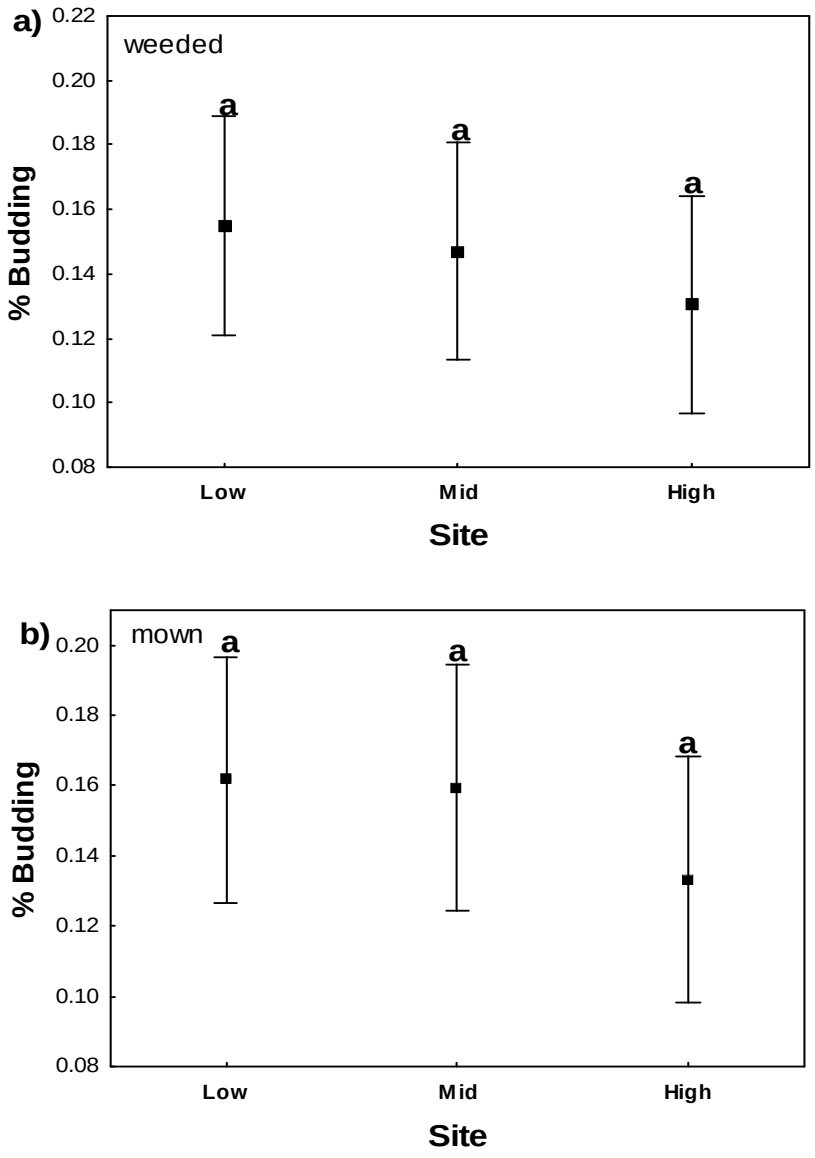


FIGURE 10. Means and 95% Confidence Intervals for General Linear Models examining the effect of altitude site on A. selago *% flower budding surface area at three altitude sites (i. e. low, mid, high), (a) weeded, (b) mown plants. Means with different letters are significantly different at $p < 0.05$ (based on an Analysis of Variance). (Means are predicted means for General Linear Models, holding treatment and month constant).*

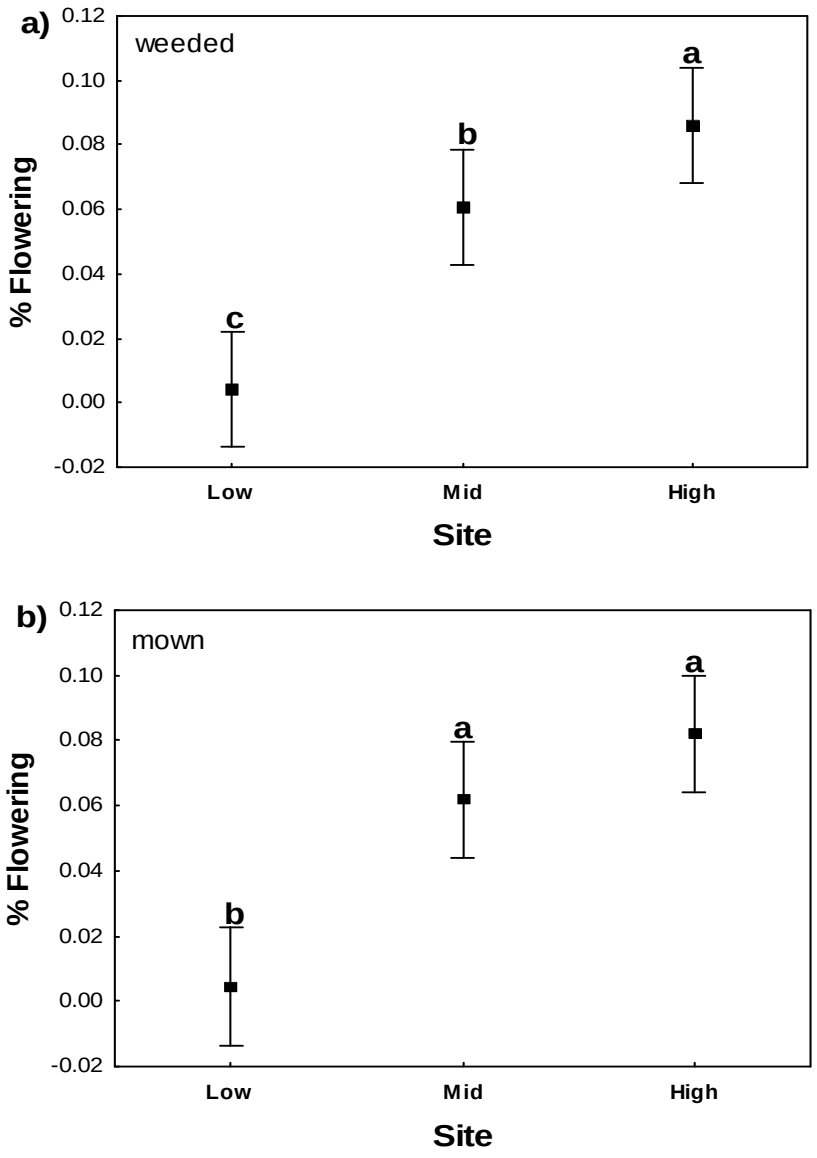


FIGURE 11. Means and 95% Confidence Intervals for General Linear Models examining the effect of altitude site on A. selago *% flowering surface area at three altitude sites (i. e. low, mid, high), (a) weeded, (b) mown plants. Means with different letters are significantly different at p < 0.05 (based on an Analysis of Variance). (Means are predicted means for General Linear Models, holding treatment and month constant).*

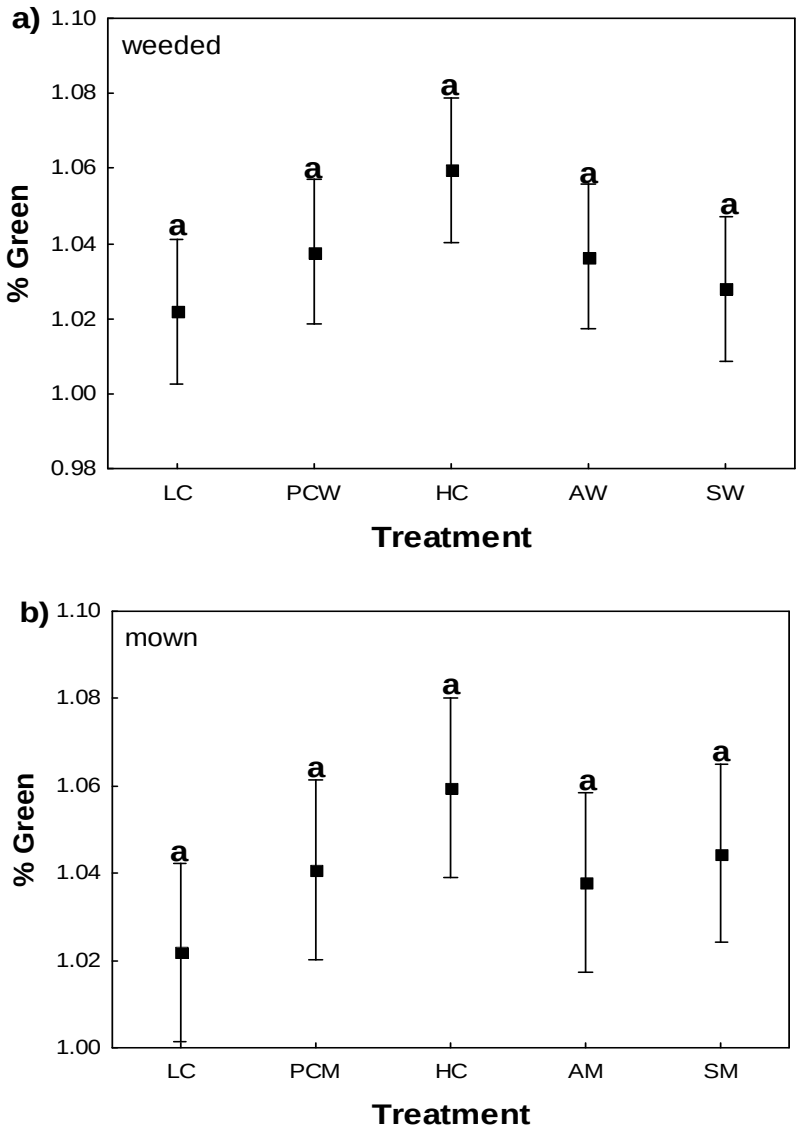


FIGURE 12. Means and 95% Confidence Intervals for General Linear Models examining the effect of treatment on A. selago *% green surface area.* Azorella selago *phenology for three different seasons (October, December, March) between treatments: HC = high grass density plants, AW = plants weeded in autumn (April/May 2005), AM = plants mown in autumn (April/May 2005), LC = low grass density, PCM = procedural control mown (5 cushions in April/May, and 5 cushions in September/October 2005), PCW = procedural control weeded plants (same as for PCM), (a) weeded, (b) mown plants. Means with different letters are significantly different at p<0.05 (based on an Analysis of Variance). (Means are predicted means from GLM's, holding month and altitude-area constant).*

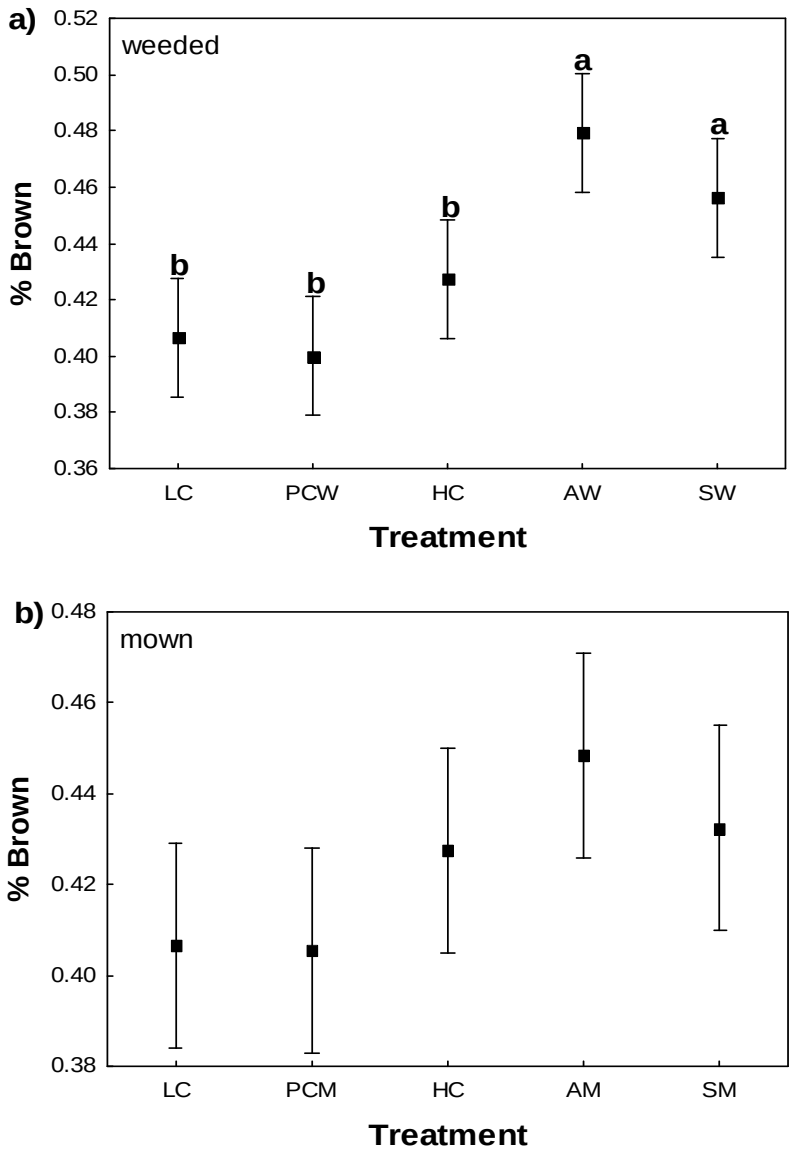


FIGURE 13. Means and 95% Confidence Intervals for General Linear Models examining the effect of treatment on A. selago *% brown surface area.* Azorella selago *phenology for three different seasons (October, December, March) between treatments: HC = high grass density plants, AW = plants weeded in autumn (April/May 2005), AM = plants mown in autumn (April/May 2005), LC = low grass density, PCM = procedural control mown (5 cushions in April/May, and 5 cushions in September/October 2005), PCW = procedural control weeded plants (same as for PCM). (a) weeded, (b) mown plants. Means with different letters are significantly different at p<0.05 (based on an Analysis of Variance). (Means are predicted means from GLM's, holding month and altitude-area constant) (letters not shown on b because multiple comparison tests were not significant).*

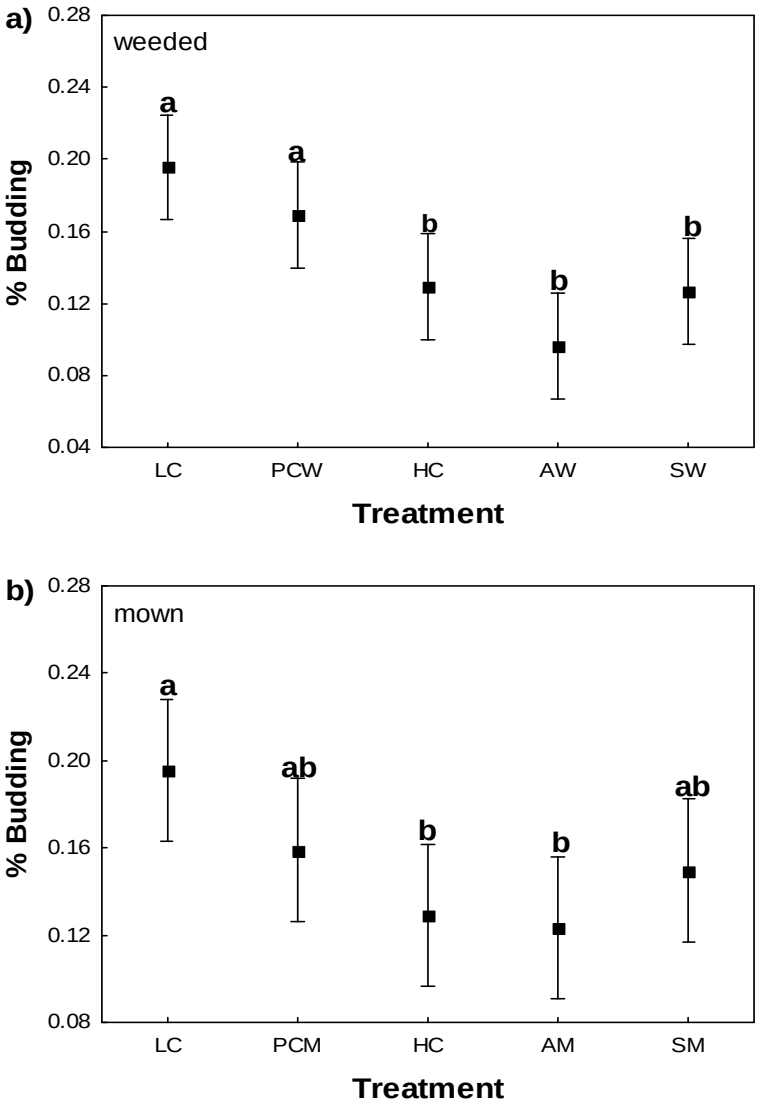


FIGURE 14. Means and 95% Confidence Intervals for General Linear Models examining the effect of treatment on A. selago *% flower budding surface area.* Azorella selago *phenology for three different seasons (October, December, March) between treatments: HC = high grass density plants, AW = plants weeded in autumn (April/May 2005), AM = plants mown in autumn (April/May 2005), LC = low grass density, PCM = procedural control mown (5 cushions in April/May, and 5 cushions in September/October 2005), PCW = procedural control weeded plants (same as for PCM). (a) weeded, (b) mown plants. Means with different letters are significantly different at $p<0.05$ (based on an Analysis of Variance). (Means are predicted means from GLM's, holding month and altitude-area constant).*

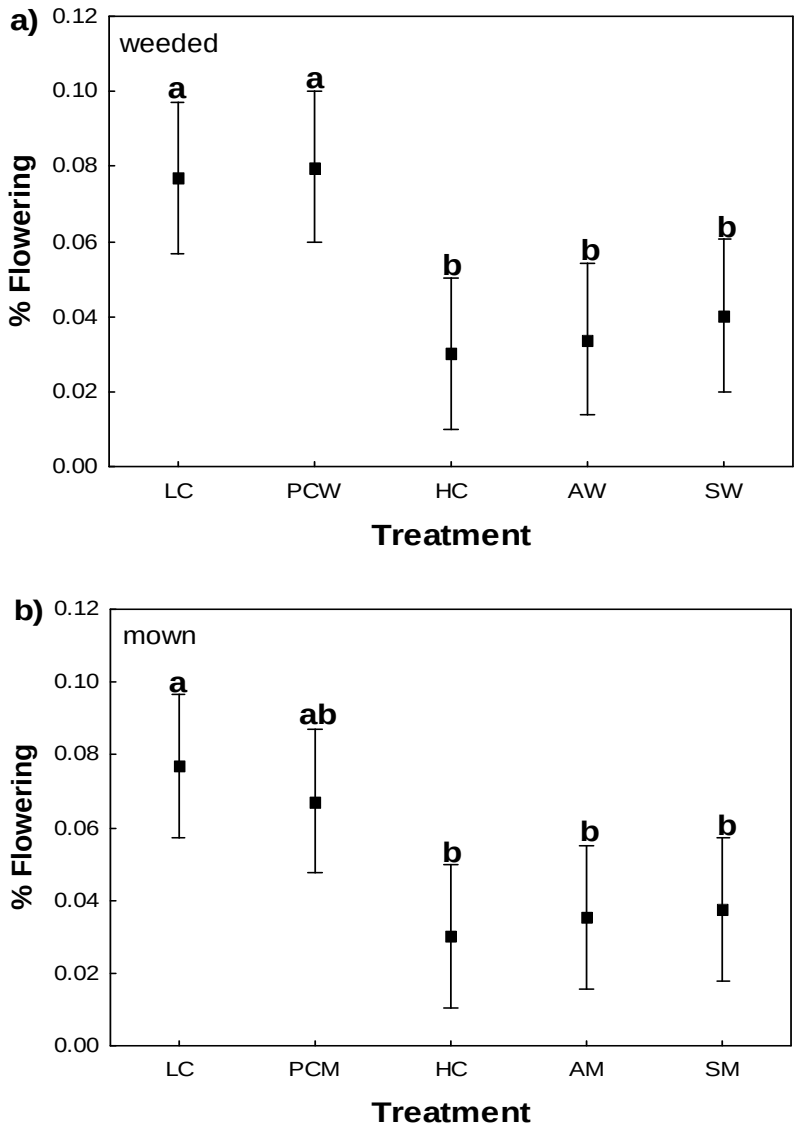


FIGURE 15. Means and 95% Confidence Intervals for General Linear Models examining the effect of treatment on A. selago *% flowering surface area.* Azorella selago *phenology for three different seasons (October, December, March) between treatments: HC = high grass density plants, AW = plants weeded in autumn (April/May 2005), AM = plants mown in autumn (April/May 2005), LC = low grass density, PCM = procedural control mown (5 cushions in April/May, and 5 cushions in September/October 2005), PCW = procedural control weeded plants (same as for PCM), (a) weeded, (b) mown plants. Means with different letters are significantly different at $p<0.05$ (based on an Analysis of Variance), (means are predicted means from GLM's, holding month and altitude-area constant).*

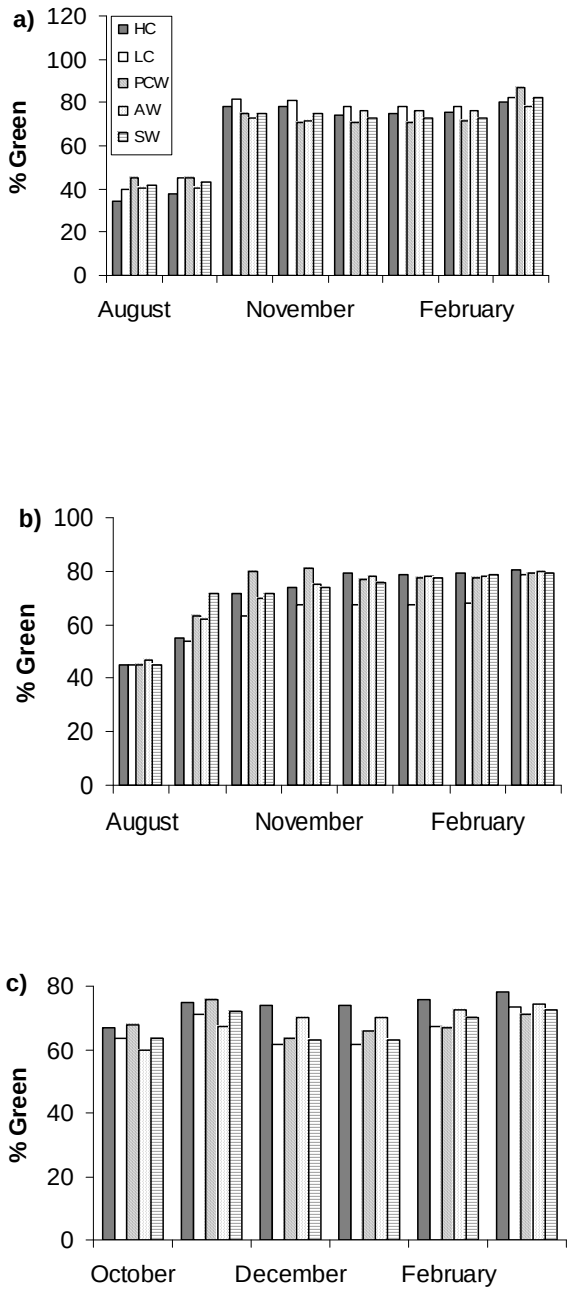


FIGURE 16. Median % green surface area of A. selago *plants at the three altitude sites, i.e. (a) low, (b) mid, (c) high altitude site, where (HC = plants with high* A. magellanica *cover, AW = plants weeded in autumn, SW = plants weeded in spring, LC = plants with low* A. magellanica *cover, PCW = procedural control weeded plants).*

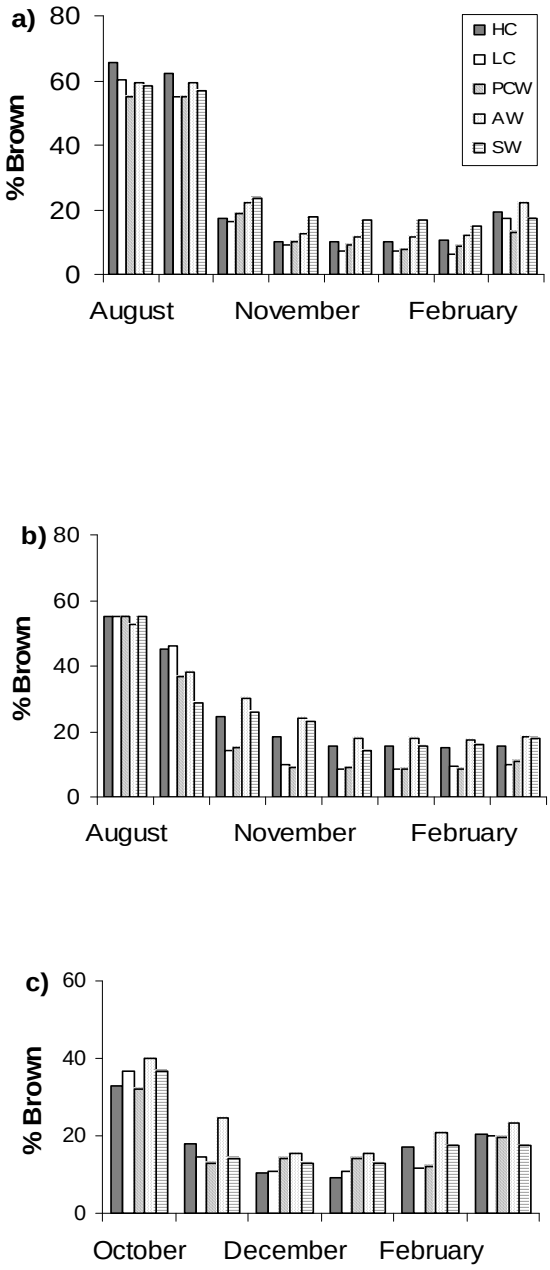


FIGURE 17. Median % brown surface area of A. selago *plants at the three altitude sites, i.e. (a) low, (b) mid, (c) high altitude site, where (HC = plants with high* A. magellanica *cover, AW = plants weeded in autumn, SW = plants weeded in spring, LC = plants with low* A. magellanica *cover, PCW = procedural control weeded plants).*

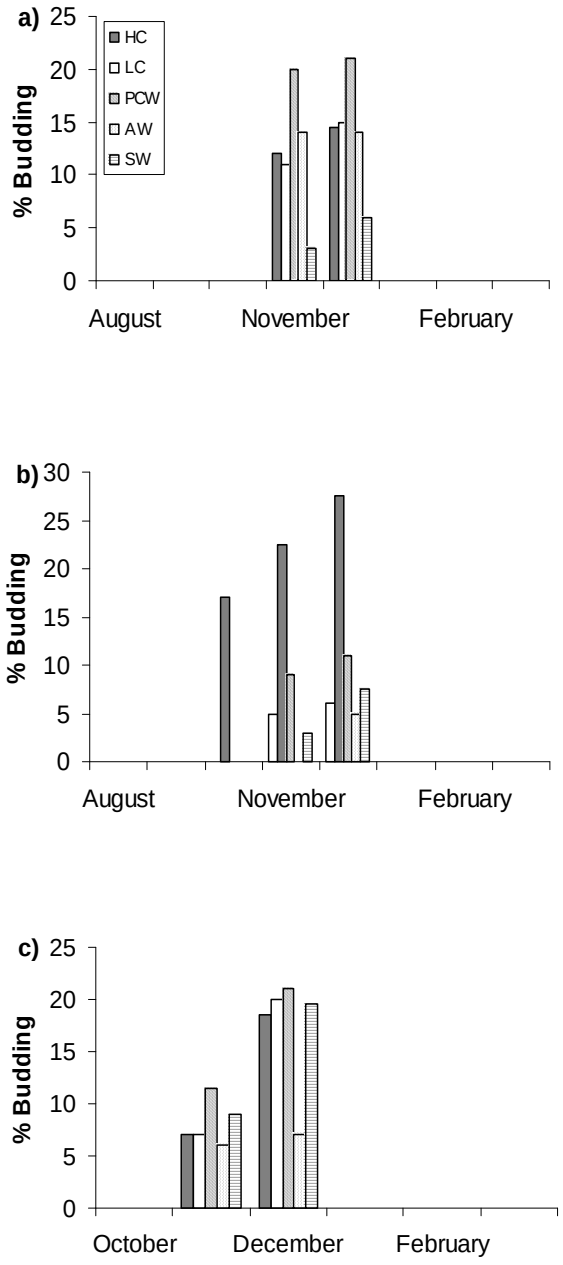


FIGURE 18. Median % of flower budding surface area of A. selago *plants at the three altitude sites, i.e. (a) low, (b) mid, (c) high altitude-area, where (HC = plants with high* A. magellanica *cover, AW = plants weeded in autumn, SW = plants weeded in spring, LC = plants with low* A. magellanica *cover, PCW = procedural control weeded plants).*

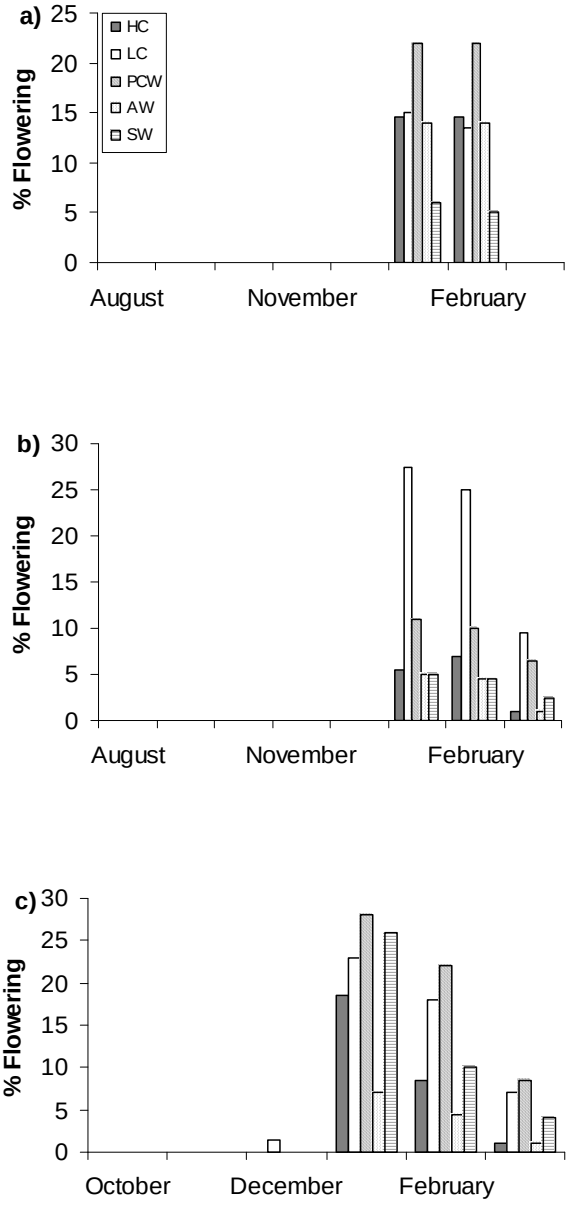


FIGURE 19. Median % flowering surface area of A. selago *plants at the three altitude sites, i.e. (a) low, (b) mid, (c) high altitude site, where (HC = plants with high* A. magellanica *cover, AW = plants weeded in autumn, SW = plants weeded in spring, LC = plants with low* A. magellanica *cover, PCW = procedural control weeded plants).*

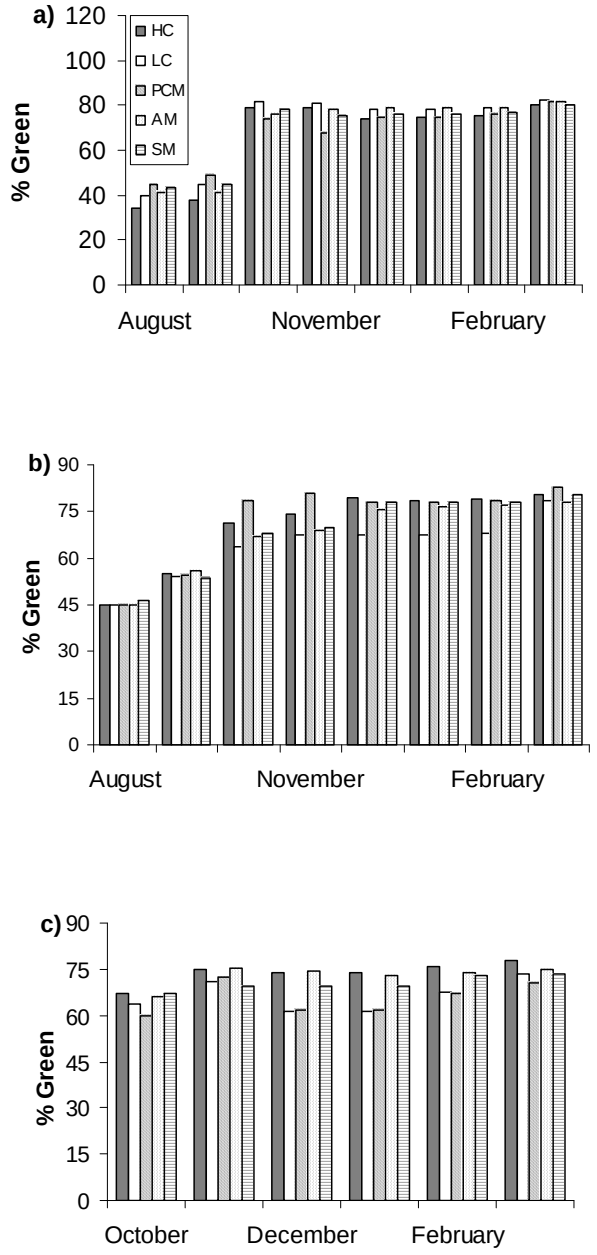


FIGURE 20. Median % green surface area of A. selago *plants at the three altitude sites, i.e. (a) low, (b) mid, (c) high altitude site, where (HC = plants with high* A. magellanica *cover, AM = plants mown in autumn, SM = plants mown in spring, LC = plants with low* A. magellanica *cover, PCM = procedural control mown plants).*

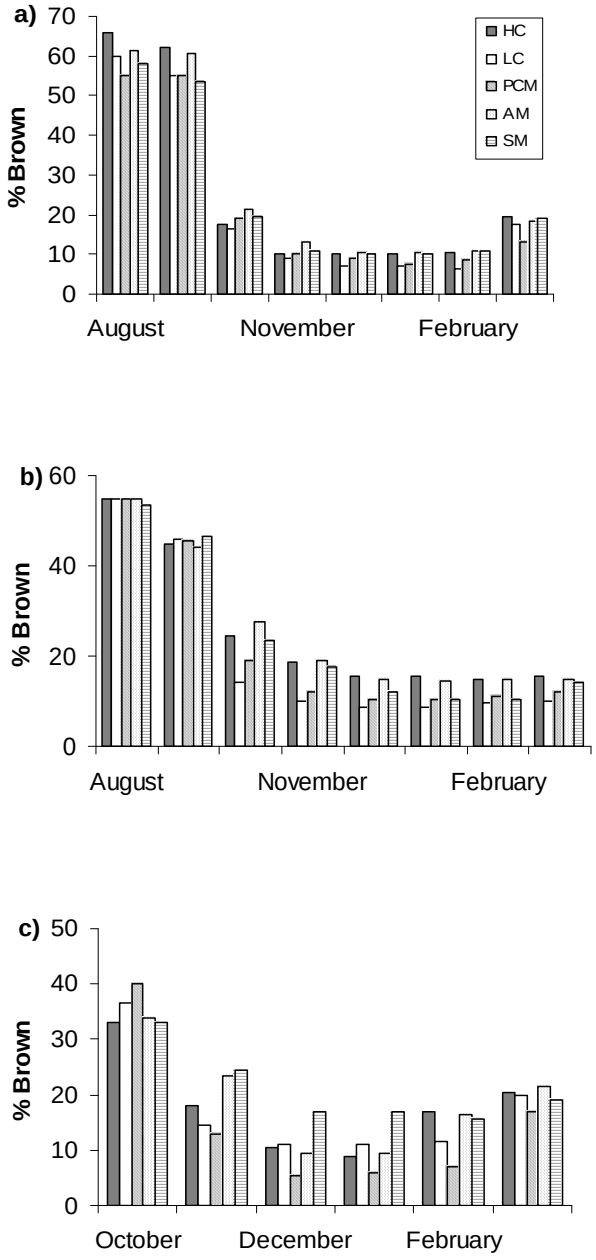


FIGURE 21. Median % brown surface area of A. selago *plants at the three altitude sites, i.e. (a) low, (b) mid, (c) high altitude site, where (HC = plants with high* A. magellanica *cover, AM = plants mown in autumn, SM = plants mown in spring, LC = plants with low* A. magellanica *cover, PCM = procedural control mown plants).*

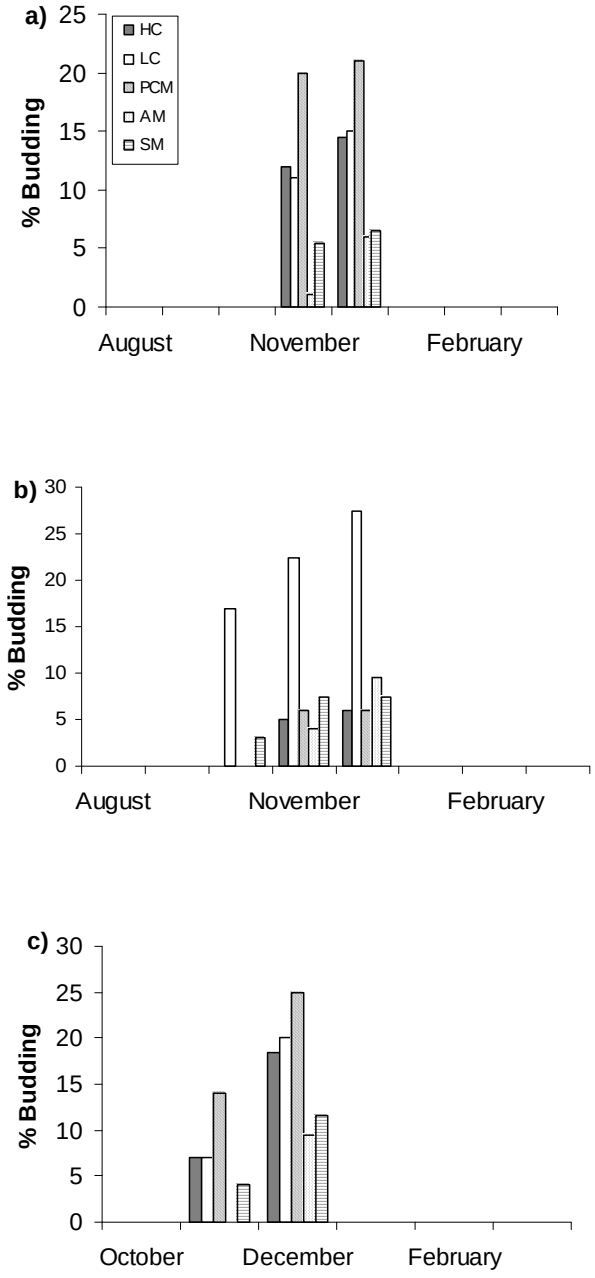


FIGURE 22. Median % flower budding surface area of A. selago *plants at the three altitude sites, i.e. (a) low, (b) mid, (c) high altitude site, where (HC = plants with high* A. magellanica *cover, AM = plants mown in autumn, SM = plants mown in spring, LC = plants with low* A. magellanica *cover, PCM = procedural control mown plants).*

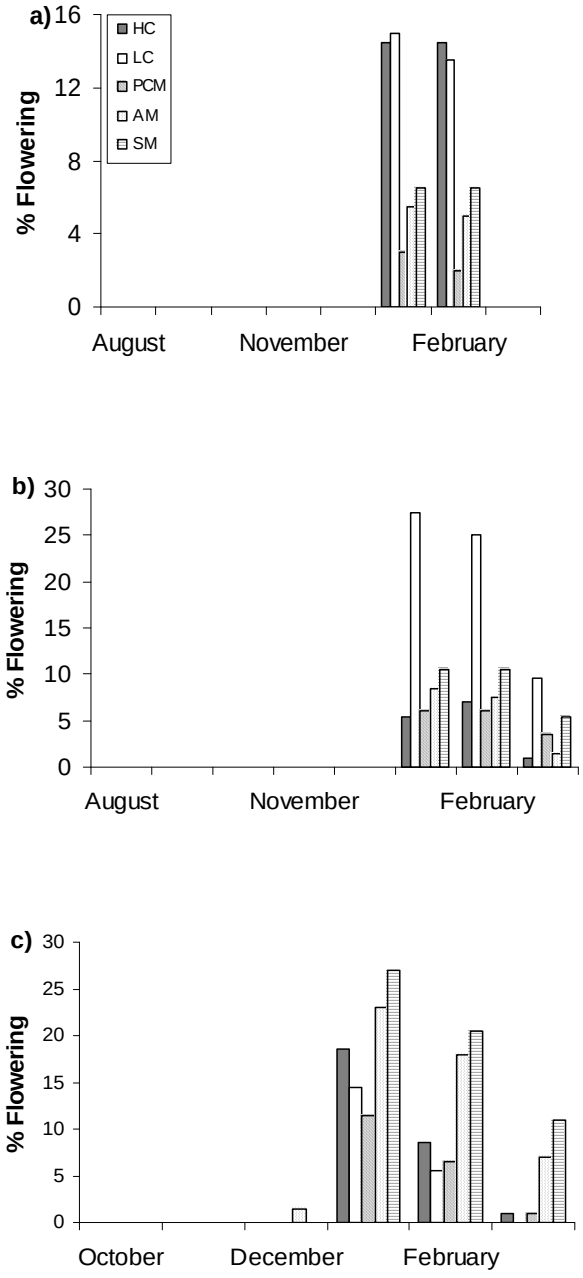


FIGURE 23. Median % flowering surface area of A. selago *plants at the three altitude sites, i.e. (a) low, (b) mid, (c) high altitude site, where (HC = plants with high* A. magellanica *cover, AM = plants mown in autumn, SM = plants mown in spring, LC = plants with low* A. magellanica *cover, PCM = procedural control mown plants).*

APPENDIX A

Daily mean temperature (℃) at three altitude sites, (Treatment 1 = plants with high Agrostis magellanica *cover, 2 = plants weeded in autumn, 4 = plants mown in autumn, 6 = plants with low* A. magellanica *cover).*

Altitude	Treatment	Mean (± s. d)	Min	Max	N (days)
May					
Low altitude	1	3.58 ± 2.60	0	12.5	18
	2	3.10 ± 3.40	-9	12.5	31
	4	4.10 ± 2.50	0	13.0	31
	6	3.52 ± 2.54	-4	11.5	19
Mid altitude	1	3.33 ± 3.01	0	10.5	5
	2	3.32 ± 3.08	0	11.0	5
	4	3.28 ± 3.10	-5	11.0	5
	6	3.53 ± 3.08	-5	10.5	5
High altitude	1	0.67 ± 0.29	0	5.0	2
	2	-0.97 ± 0.79	-9	3.0	2
	4	0.22 ± 0.06	0	1.0	2
	6	0.16 ± 0.15	-1	2.0	2
June					
Low altitude	1	4.70 ± 2.54	-0.5	11.5	30
	2	4.54 ± 3.20	-10.5	11.0	30
	4	4.80 ± 2.44	0	12.0	30
	6	4.68 ± 2.59	-0.5	11.0	30
Mid altitude	1	4.48 ± 2.64	-0.5	11.5	30
	2	4.45 ± 2.64	-1.5	11.0	30
	4	4.51 ± 2.63	-0.5	11.5	30
	6	4.80 ± 2.59	-0.5	11.0	30
High altitude	1	3.83 ± 2.53	-0.5	10.5	30

APPENDIX A continued

Daily mean temperature (℃) at three altitude sites, (Treatment 1 = plants with high Agrostis magellanica *cover, 2 = plants weeded in autumn, 4 = plants mown in autumn, 6 = plants with low* A. magellanica *cover).*

Altitude	Treatment	Mean (± s. d)	Min	Max	N (days)
	2	3.34 ± 3.40	-10	12.0	30
	4	3.72 ± 2.64	-0.5	11.5	30
	6	3.65 ± 2.80	-1	11.5	30
July					
Low altitude	1	3.13 ± 2.36	-2	8.5	31
	2	2.50 ± 3.34	-11	8.5	31
	4	3.19 ± 2.27	-1	8.0	31
	6	3.06 ± 2.42	-1.5	8.0	31
Mid altitude	1	2.66 ± 2.22	-1.5	7.5	31
	2	2.56 ± 2.24	-1.5	7.5	31
	4	2.61 ± 2.22	-2	7.5	31
	6	3.87 ± 2.21	-2	7.5	31
High altitude	1	2.05 ± 1.81	0	6.5	31
	2	0.90 ± 2.83	-10	7.5	31
	4	1.81 ± 1.90	-1	6.5	31
	6	1.56 ± 2.00	-2	7.0	31
August					
Low altitude	1	3.49 ± 2.71	-1.5	11.0	31
	2	3.10 ± 3.39	-10	10.5	31
	4	3.54 ± 2.59	-1	11.0	31
	6	3.40 ± 2.75	-1	10.5	31
Mid altitude	1	3.01 ± 2.60	-1	11.0	31
	2	2.89 ± 2.60	-1.5	10.5	31
	4	2.96 ± 2.56	-1	10.0	31
	6	3.22 ± 2.55	-1	10.0	31
High altitude	1	2.36 ± 2.32	-1.5	13.5	31

APPENDIX A continued

Daily mean temperature (℃) at three altitude sites, (Treatment 1 = plants with high Agrostis magellanica *cover, 2 = plants weeded in autumn, 4 = plants mown in autumn, 6 = plants with low* A. magellanica *cover).*

Altitude	Treatment	Mean (± s. d)	Min	Max	N (days)
	2	1.67 ± 3.08	-10.5	12.0	31
	4	2.09 ± 2.43	-1.5	12.5	31
	6	2.01 ± 2.59	-2	12.5	31
September					
Low altitude	1	4.71 ± 3.73	-0.5	19.0	10
	2	4.70 ± 3.75	-2.5	20.0	10
	4	4.33 ± 3.64	-0.5	17.5	10
	6	4.63 ± 4.39	-0.5	19.0	10
Mid altitude	1	3.41 ± 3.73	-1	17.5	24
	2	3.26 ± 3.69	-1	17.5	24
	4	3.29 ± 3.64	-1	17.5	24
	6	3.57 ± 3.53	-1	17.5	24
High altitude	1	3.37 ± 2.50	-2	16.5	30
	2	1.91 ± 3.06	-10.5	15.0	30
	4	2.11 ± 2.57	-2	15.0	30
	6	2.13 ± 2.82	-2	15.0	30
October					
Low altitude	1	4.75 ± 2.61	0	18.0	9
	2	4.59 ± 2.38	-7	10.0	9
	4	4.86 ± 2.59	0	14.5	9
	6	4.85 ± 2.37	0	10.5	9
	2	4.60 ± 3.50	-9	17.5	31
	4	4.69 ± 3.24	-0.5	17.5	31
	6	4.78 ± 3.73	-1	18.0	31
Nov					
Low altitude	1	7.52 ± 3.68	0.5	23.0	30

APPENDIX A continued

Daily mean temperature (℃) at three altitude sites, (Treatment 1 = plants with high Agrostis magellanica *cover, 2 = plants weeded in autumn, 4 = plants mown in autumn, 6 = plants with low* A. magellanica *cover).*

Altitude	Treatment	Mean (± s. d)	Min	Max	N (days)
	2	7.20 ± 3.34	1	21.0	30
	4	7.45 ± 3.67	0.5	22.0	30
	6	7.41 ± 3.38	0.5	21.0	30
Mid altitude	1	7.21 ± 3.45	1	20.0	30
	2	7.11 ± 3.54	1	20.0	30
	4	7.05 ± 3.14	1	18.5	30
	6	7.36 ± 3.56	1.5	18.5	30
December					
Low altitude	1	9.14 ± 3.61	1.5	25.5	31
	2	8.70 ± 3.20	1.5	22.5	31
	4	9.09 ± 3.61	1.5	24.5	31
	6	8.96 ± 3.21	1	22.0	31
Mid altitude	1	9.11 ± 3.66	1.5	23.0	31
	2	8.95 ± 3.84	1.5	23.5	31
	4	8.98 ± 3.49	2	22.0	31
	6	9.14 ± 3.71	1.5	21.5	31
High altitude	1	8.68 ± 3.91	2	22.5	14
	2	8.23 ± 4.23	1	23.0	14
	4	8.50 ± 3.94	0	23.5	14
	6	8.57 ± 4.27	1.5	23.0	14
January					
Low altitude	1	8.89 ± 3.73	1	24.5	31
	2	8.44 ± 3.44	1	23.0	31
	4	8.79 ± 3.82	1	23.5	31
	6	8.60 ± 3.35	1	22.5	31

APPENDIX A continued

Daily mean temperature (℃) at three altitude sites, (Treatment 1 = plants with high Agrostis magellanica *cover, 2 = plants weeded in autumn, 4 = plants mown in autumn, 6 = plants with low* A. magellanica *cover).*

Altitude	Treatment	Mean (± s. d)	Min	Max	N (days)
Mid altitude	1	8.62 ± 3.63	1.5	22.0	31
	2	8.51 ± 3.81	1.5	23.0	31
	4	8.60 ± 3.38	2	20.5	31
	6	8.61 ± 3.67	1.5	21.0	31
High altitude	1	7.96 ± 3.60	0	21.5	31
	2	7.50 ± 3.92	0	22.0	31
	4	7.74 ± 3.61	0.5	21.5	31
	6	7.63 ± 3.96	0	22.5	31
February					
Low altitude	1	9.17 ± 3.55	1.5	26.0	28
	2	8.94 ± 3.24	1.5	21.5	28
	4	9.22 ± 3.66	1.5	25.5	28
	6	8.94 ± 3.10	1.5	21.0	28
Mid altitude	1	8.63 ± 3.18	1	20.0	28
	2	8.48 ± 3.31	1.5	19.0	28
	4	8.57 ± 2.94	1.5	19.0	28
	6	8.63 ± 3.21	1.5	20.0	28
High altitude	1	7.57 ± 3.08	1.5	19.5	28
	2	7.12 ± 3.39	0	19.5	28
	4	7.36 ± 3.09	0.5	21.0	28
	6	7.22 ± 3.38	0	21.0	28
March					
Low altitude	1	9.38 ± 4.78	1	26.5	20
	2	9.39 ± 4.89	1	26.0	20
	4	9.57 ± 4.90	1	26.5	20

APPENDIX A continued

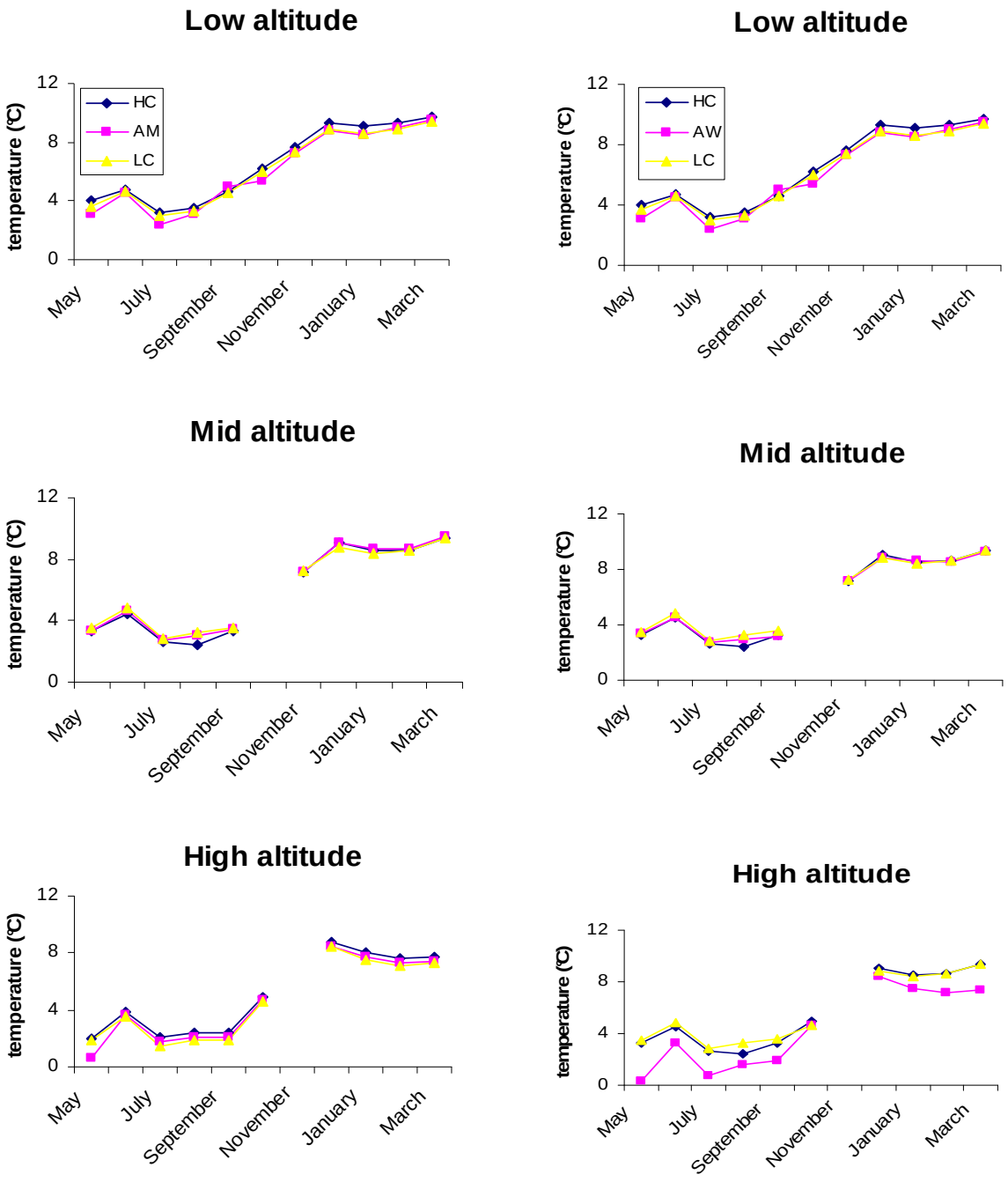
Daily mean temperature (℃) at three altitude sites, (Treatment 1 = plants with high Agrostis magellanica *cover, 2 = plants weeded in autumn, 4 = plants mown in autumn, 6 = plants with low* A. magellanica *cover).*

Altitude	Treatment	Mean (± s. d)	Min	Max	N (days)
Low altitude	6	9.41 ± 4.79	0.5	26.0	20
Mid altitude	1	9.36 ± 4.71	1	21.5	11
	2	9.40 ± 4.80	1	21.0	11
	4	8.60 ± 3.38	2	20.5	31
	6	8.61 ± 3.67	1.5	21.0	31
High altitude	1	7.96 ± 3.60	0	21.5	31
	2	7.50 ± 3.92	0	22.0	31
	4	7.74 ± 3.61	0.5	21.5	31
	6	7.63 ± 3.96	0	22.5	31
February					
Low altitude	1	9.17 ± 3.55	1.5	26.0	28
	2	8.94 ± 3.24	1.5	21.5	28
	4	9.22 ± 3.66	1.5	25.5	28
	6	8.94 ± 3.10	1.5	21.0	28
Mid altitude	1	8.63 ± 3.18	1	20.0	28
	2	8.48 ± 3.31	1.5	19.0	28
	4	8.57 ± 2.94	1.5	19.0	28
	6	8.63 ± 3.21	1.5	20.0	28
High altitude	1	7.57 ± 3.08	1.5	19.5	28
	2	7.12 ± 3.39	0	19.5	28
	4	7.36 ± 3.09	0.5	21.0	28
	6	7.22 ± 3.38	0	21.0	28
March					
Low altitude	1	9.38 ± 4.78	1	26.5	20
	2	9.39 ± 4.89	1	26.0	20

APPENDIX A continued

Daily mean temperature (℃) at three altitude sites, (Treatment 1 = plants with high Agrostis magellanica *cover, 2 = plants weeded in autumn, 4 = plants mown in autumn, 6 = plants with low* A. magellanica *cover).*

Altitude	Treatment	Mean (± s. d)	Min	Max	N (days)
March					
Low altitude	4	9.57 ± 4.90	1	26.5	20
	6	9.41 ± 4.79	0.5	26.0	20
Mid altitude	1	9.36 ± 4.71	1	21.5	11
	2	9.40 ± 4.80	1	21.0	11
	4	9.27 ± 4.34	1.5	20.5	11
	6	9.40 ± 4.50	1	20.5	11
High altitude	1	7.69 ± 3.83	-5	20.5	14
	2	7.37 ± 4.10	0	20.0	14
	4	7.44 ± 3.75	0	19.0	14
	6	7.40 ± 3.96	0	20.0	14



APPENDIX B. Mean temperatures inside A. selago *cushions at three areas for the given months, HC = control plants with high epiphyte cover, AW = cushions weeded in autumn, AM = cushions mown in autumn, LC = control plants with low epiphyte cover (n = 5 plants, error bars excluded for clarity see Appendix A - H).*

APPENDIX C

Differences in A. selago *phenology for three different seasons (October, December, March), i.e % brown, % flower buds, % flowering surface area between treatments (HC = high grass density plants, AW = plants weeded in autumn, AM = plants mown in autumn, LC = low grass density, PCM = procedural control mown, PCW = procedural control weeded plants), (means and standard errors for the GLM model examining the effect of treatments on plants). All percentages were transformed using square root arcsine, n = 150. Means with different letters in superscript are significantly different at p < 0.05 (based on Analysis of Variance). (See table 4).*

Phenological traits	Treatment	mean ± s. e
Weeded		
%Brown	AW	0.48 ± 0.01^{a}
	SW	0.45 ± 0.01^{a}
	HC	0.42 ± 0.01^{b}
	LC	0.40 ± 0.01^{b}
	PCW	0.39 ± 0.01^{b}
%Budding	LC	0.19 ± 0.01^{a}
	PCW	0.17 ± 0.01^{a}
	SW	0.12 ± 0.01^{b}
	HC	0.12 ± 0.01^{b}
	AW	0.10 ± 0.01^{b}
%Flowering	PCW	0.08 ± 0.009^{a}
	LC	0.07 ± 0.009^{a}
	SW	0.04 ± 0.009^{b}
	AW	0.02 ± 0.009^{b}
	HC	0.02 ± 0.009^{b}
Mown		
%Brown	AM	0.44 ± 0.01
	SM	0.43 ± 0.01
	HC	0.42 ± 0.01
	LC	0.40 ± 0.01

APPENDIX C continued

Differences in A. selago *phenology for three different seasons (October, December, March), i.e % brown, % flower buds, % flowering surface area between treatments (HC = high grass density plants, AW = plants weeded in autumn, AM = plants mown in autumn, LC = low grass density, PCM = procedural control mown, PCW = procedural control weeded plants), (means and standard errors for the GLM model examining the effect of treatments on plants). All percentages were transformed using square root arcsine, n = 150. Means with different letters in superscript are significantly different at $p < 0.05$ (based on Analysis of Variance). (See table 4).*

Phenological traits	Treatment	mean ± s. e
%Brown	PCM	0.40 ± 0.01
%Budding	LC	0.19 ± 0.01^{a}
	PCM	0.15 ± 0.01^{ab}
	SM	0.14 ± 0.01^{ab}
	HC	0.12 ± 0.01^{b}
	AM	0.12 ± 0.01^{b}
%Flowering	LC	0.07 ± 0.01^{a}
	PCM	0.06 ± 0.01^{ab}
	SM	0.03 ± 0.01^{b}
	AM	0.03 ± 0.01^{b}
	HC	0.03 ± 0.01^{b}

APPENDIX D

Phenological traits for 10 control Azorella selago *plants with high* Agrostis magellanica *cover (1T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
1T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Aug 2004	34.25 (20-57)	45 (35-58)	-	65.75 (43-80)	55 (42-75)	-	0	0	_	0	0	_
Sept 2004	38 (25-60)	55 (45-84)	-	62 (40-75)	45 (16-55)	-	0	0	_	0	0	_
Oct 2004	78.5 (59-88)	71.5 (48-89)	67 (50-80)	17.5 (12-25)	24.5 (11-45)	33 (20-50)	0 (0-24)	0 (0 -34)	0	0	0	0
Nov 2004	78.5 (61-89)	74 (54-85)	75 (69-80)	10 (6- 25)	18.5 (5-32)	18 (1- 25)	12 (0- 29)	5 (0 - 6)	7 (0 -9)	0	0	0

APPENDIX D continued

Phenological traits for 10 control Azorella selago plants with high Agrostis magellanica *cover (1T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
1T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Dec 2004	74 (53-90)	79.5 (54-86)	74 (59 - 83)	10 (4-16)	15.5 (4-22)	10.5 (1-22)	14.5 (0-27)	6 (0 - 36)	18.5 (0 -24)	0	0	0
Jan 2005	75 (53-90)	78.5 (54-86)	74 (60 -83)	10 (4-16)	15.5 (4-22)	9 (1-22)	0	0	0	14.5 (0-37)	5.5 (0-36)	18.5 (0- 30)
Feb 2005	75.5 (54-90)	79 (55-87)	76 (67-83)	10.5 (4-17)	15 (4-22)	17 (1-21)	0	0	0	14.5 (0-34)	7 (0 - 34)	8.5 (0 - 30)
March 2005	80.5 (70-90)	80.5 (75-87)	78 (71-83)	19.5 (4-30)	15.5 (10-22)	20.5 (10-26)	0	0	0	0 (0-15)	1 (0 - 10)	1 (0 - 10)

APPENDIX E

Phenological traits for 10 Azorella selago *plants weeded in autumn (2T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
2T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Aug 2004	40.5 (18-53)	46.5 (30-57)	-	59.5 (47-82)	52.5 (42-70)	-	0	0	_	0	0	_
Sept 2004	40.5 (22-52)	62 (45-75)	-	59.5 (48-78)	38 (25-55)	-	0	0	_	0	0	_
Oct 2004	72.5 (51-90)	70 (58-77)	60 (50-80)	22 (8-49)	30 (16-49)	40 (20-50)	0 (0-23)	0 (0 - 12)	0	0	0	0
Nov 2004	71.5 (66-86)	75 (65-80)	67.5 (56-85)	12.5 (8-22)	24 (15-35)	24.5 (15-44)	14 (0-22)	1 (0 - 15)	6 (0 - 18)	0	0	0

APPENDIX E continued

Phenological traits for 10 Azorella selago *plants weeded in autumn (2T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
2T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Dec 2004	76 (66-87)	78 (69-81)	70 (58-85)	11.5 (7-20)	18 (10-25)	15.5 (9-35)	14 (1-22)	5 (0 - 15)	7 (0 - 21)	0	0	0 (0-12)
Jan 2005	76 (66-87)	78 (69-81)	70 (58-85)	11.5 (7-20)	18 (10-25)	15.5 (9-35)	0	0	0	14 (1-22)	5 (0-15)	7 (0 -26)
Feb 2005	76.5 (66-87)	78 (71-82)	72.5 (62-88)	12 (6-20)	17.5 (10-25)	21 (9-28)	0	0	0	14 (1-23)	4.5 (0-12)	4.5 (0-21)
March 2005	78 (75-87)	80 (75-85)	74.5 (67-88)	22 (13-25)	18.5 (10-25)	23.5 (15-28)	0	0	0	0	1 (0 - 5)	1 (0 - 8)

APPENDIX F

Phenological traits for10 Azorella selago *plants weeded in spring (3T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
3T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Aug 2004	41.5 (23 - 49)	45 (25 - 54)	-	58.5 (51 - 77)	55 (46 - 75)	-	0	0	_	0	0	_
Sept 2004	43.25 (35 - 55)	71.5 (44 - 80)	-	56.75 (44 - 65)	28.5 (20 - 56)	-	0	0	_	0	0	_
Oct 2004	75 (59 - 84)	71.5 (61 - 83)	63.5 (55 - 78)	23.5 (16 - 37)	26 (12 - 39)	36.5 (22 - 45)	0 (0 - 24)	0 (0 - 9)	0	0	0	0
Nov 2004	74.5 (61 - 87)	74 (65 - 85)	72 (60 - 85)	18 (8 - 36)	23 (5 - 34)	14 (6 - 23)	3 (0 - 29)	3 (0 - 15)	9 (0 - 30)	0	0	0

APPENDIX F continued

Phenological traits for10 Azorella selago *plants weeded in spring (3T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
3T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Dec 2004	72.5 (53 - 87)	76 (66 - 84)	63 (53 - 77)	17 (8 - 30)	14 (5 - 29)	13 (4 - 23)	6 (0 - 37)	7.5 (0 - 15)	19.5 (0 - 40)	0	0	0 (0 - 7)
Jan 2005	72.5 (54 - 87)	77.5 (66 - 84)	63 (53 - 77)	17 (8 - 30)	15.5 (6 - 29)	13 (4 - 23)	0	0	0	6 (0 - 36)	5 (0 - 15)	26 (0 - 40)
Feb 2005	73 (60 - 87)	78.5 (69 - 85)	70 (59 - 77)	15 (3 - 30)	16 (5 - 26)	17.5 (8 - 25)	0	0	0	5 (0 - 30)	4.5 (0 - 15)	10 (0 - 30)
March 2005	82.5 (75 - 90)	79 (72 - 84)	72.5 (61 - 80)	17.5 (10 - 25)	18 (13 - 26)	17.5 (8 - 25)	0	0	0	0	2.5 (0 - 7)	4 (0 - 24)

APPENDIX G

Phenological traits for10 Azorella selago *plants mown in autumn (4T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
4T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Aug 2004	41 (3 - 55)	45 (39 - 57)	-	61.25 (46 - 97)	55 (41 - 61)	-	0	0	_	0	0	_
Sept 2004	41 (3 - 55)	56 (45 - 75)	-	60.5 (50 - 97)	44 (25 - 55)	-	0	0	_	0	0	_
Oct 2004	76 (55 - 84)	67 (48 - 75)	66 (53 - 78)	21.5 (6 - 45)	27.5 (12 - 45)	34 (22 - 47)	0 (0 - 24)	0 (0 - 34)	0	0	0	0
Nov 2004	78 (63 - 90)	69 (55 - 84)	75.5 (72 - 81)	13 (6 - 25)	19 (5 - 40)	23.5 (6-25)	1 (0 - 29)	4 (0 - 35)	0 (0 - 13)	0	0	0

APPENDIX G continued

Phenological traits for10 Azorella selago *plants mown in autumn (4T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
4T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Dec 2004	78.5 (57 - 88)	75.5 (55 - 83)	74.5 (59 - 88)	10.5 (6 - 22)	15 (5 - 25)	9.5 (4 - 25)	6 (0 - 35)	9.5 (0 - 35)	19.5 (0 - 35)	0	0	0 (0 - 12)
Jan 2005	78.5 (57 - 89)	76.5 (60 - 83)	73 (60 - 88)	10.5 (6 - 22)	14.5 (5 - 25)	9.5 (4 - 25)	0	0	0	5.5 (0 - 35)	8.5 (0 - 30)	14.5 (0 - 33)
Feb 2005	79 (60 - 89)	77 (65 - 84)	74 (60 - 84)	11 (6 - 22)	15 (6 - 25)	16.5 (6 - 25)	0	0	0	5 (0 - 30)	7.5 (0 - 25)	5.5 (2 - 33)
March 2005	81.5 (70 - 94)	78 (36 - 89)	75 (66 - 84)	18.5 (6 - 30)	15 (8 - 25)	21.5 (11 - 30)	0	0	0	0	1.5 (0 - 9)	0 (0 - 23)

APPENDIX H

Phenological traits for10 Azorella selago *plants mown in spring (5T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
5T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Aug 2004	43 (22 - 51)	46.5 (24 - 55)	-	58 (50.5 - 78)	53.5 (42 - 76)	-	0	0	_	0	0	_
Sept 2004	45 (35 - 55)	53.5 (37 - 82)	-	53.5 (45 - 65)	46.5 (20 - 63)	-	0	0	_	0	0	_
Oct 2004	78 (50 - 85)	68 (55 - 80)	67 (50 - 83)	19.5 (6 - 50)	23.5 (6 - 45)	33 (17 - 50)	0 (0 - 28)	3 (0 - 26)	0	0	0	0
Nov 2004	75.5 (61 - 88)	70 (60 - 82)	69.5 (58 - 83)	11 (6 - 29)	17.5 (6 - 40)	24.5 (13 - 31)	5.5 (0 - 29)	7.5 (0 - 28)	4 (0 - 18)	0	0	0

APPENDIX H continued

Phenological traits for10 Azorella selago *plants mown in spring (5T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
5T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Dec 2004	76 (53 - 87)	70 (60 - 82)	69.5 (59 - 83)	10 (6 - 25)	12 (4 - 25)	17 (6 - 31)	6.5 (0 - 37)	7.5 (0 - 30)	11.5 (0 - 35)	0	0	0
Jan 2005	76 (53 - 87)	78 (65 - 90)	69.5 (59 - 83)	10 (6 -25)	10.5 (4 - 20)	17 (6 - 31)	0	0 (0 - 2)	0	6.5 (0 - 37)	10.5 (0 - 30)	11.5 (0 - 35)
Feb 2005	77 (56 - 87)	78 (66 - 90)	73 (62 - 83)	11 (6 - 23)	10.5 (4 - 19)	15.5 (8 - 31)	0	0	0	6.5 (0 - 32)	10.5 (0 - 26)	6.5 (0 - 30)
March 2005	80 (75 - 90)	80.5 (70 - 90)	73.5 (69 - 83)	19 (10 - 25)	14 (10-20)	19 (14 - 31)	0	0	0	0 (0 - 3)	5.5 (0 - 15)	1 (0 - 15)

APPENDIX I

Phenological traits for 10 Azorella selago *plants with low* A. magellanica *cover (6T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
6T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Aug 2004	40 (20 - 48)	45 (21 - 50)	-	60 (52 - 80)	55 (42 - 79)	-	0	0	_	0	0	_
Sept 2004	45 (20 - 50)	54 (40 - 84)	-	55 (50 - 80)	46 (16 - 60)	-	0	0	_	0	0	_
Oct 2004	81.5 (60 - 90)	63.5 (47 - 82)	63.5 (56 - 82)	16.5 (7 - 40)	14 (6 - 38)	36.5 (20 - 44)	0 (0 - 24)	17 (0 - 39)	0	0	0	0
Nov 2004	81 (61 - 90)	67.5 (50 - 82)	71 (60 - 80)	9 (2 - 20)	10 (5 - 30)	14.5 (10 - 40)	11 (0 - 29)	22.5 (0 - 40)	7 (0 - 30)	0	0	0

APPENDIX I continued

Phenological traits for 10 Azorella selago *plants with low* A. magellanica *cover (6T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
6T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Dec 2004	78 (61 -85)	67.5 (53 - 80)	61.5 (50 - 78)	7 (3 - 20)	8.5 (5 - 20)	11 (4 - 25)	15 (0 - 29)	27.5 (0 - 40)	20 (10 - 30)	0	0	1.5 (0-11)
Jan 2005	78 (61 - 85)	67.5 (53 - 81)	61.5 (55 - 78)	7 (3 - 20)	8.5 (5 - 20)	11 (4 - 25)	0	0	0	15 (0 - 29)	27.5 (0 - 40)	23 (12 -31)
Feb 2005	78.5 (61 - 85)	68 (56 - 81)	67.5 (59 - 78)	6.5 (3- 20)	9.5 (5 - 0)	11.5 (4 - 27)	0	0	0	13.5 (0 - 29)	25 (0 - 35)	18 (2 - 35)
March 2005	82.5 (75 - 90)	78.5 (69 - 87)	73.5 (63 - 79)	17.5 (10 - 25)	10 (8 - 20)	20 (7 - 30)	0	0	0	0 (0 - 1)	9.5 (0 - 23)	7 (0 - 30)

APPENDIX J

Phenological traits for 10 procedural control weeded Azorella selago *plants (7T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
7T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Aug 2004	45 (36 - 77)	45 (15 - 57)	-	55 (23 - 64)	55 (43 - 85)	-	0	0	_	0	0	_
Sept 2004	45 (38 - 78)	63.5 (50 - 84)	-	55 (22 - 62)	36.5 (16 - 50)	-	0	0	_	0	0	_
Oct 2004	75 (64 - 92)	80 (68 - 85)	68 (50 - 74)	19 (1 - 36)	15 (6 - 32)	32 (26 - 50)	0 (0 - 26)	0 (0 - 26)	0	0	0	0
Nov 2004	70.5 (61 - 85)	81 (65 - 87)	76 (60 - 80)	10 (0 - 23)	9 (2 - 27)	13 (2 - 25)	20 (0 - 30)	9 (0 - 26)	11.5 (0 - 30)	0	0	0

APPENDIX J continued

Phenological traits for 10 procedural control weeded Azorella selago *plants (7T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
7T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Dec 2004	70.5 (53 - 86)	77 (65 - 87)	63.5 (56 - 75)	9 (2 - 15)	9 (2 - 27)	14 (4 - 25)	21 (6 - 37)	11 (5 - 28)	21 (0 - 38)	0	0	0 (0 - 11)
Jan 2005	70.5 (53 - 86)	77.5 (65 - 87)	66 (56 - 75)	7.5 (2 - 15)	8.5 (2 - 27)	14 (4 - 25)	0	0	0	22 (6 - 36)	11 (5 - 28)	28 (0 - 38)
Feb 2005	71.5 (54 - 87)	77.5 (66 - 87)	67 (56 - 75)	8.5 (2 - 13)	8.5 (2 - 27)	12 (5 - 22)	0	0	0	22 (4 - 34)	10 (5 - 27)	22 (6 - 34)
March 2005	87 (75 - 90)	79 (70 - 87)	71 (62 - 79)	13 (10 - 25)	11 (5 - 25)	19.5 (5 - 25)	0	0	0	0 (0 - 2)	6.5 (5 - 20)	8.5 (0 - 30)

APPENDIX K

Phenological traits for 10 procedural control mown Azorella selago *plants (8T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
8T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Aug 2004	44.5 (39 - 62)	45 (15 - 52)	-	55.5 (38 - 61)	55 (44 - 85)	-	0	0	_	0	0	_
Sept 2004	49 (40 - 68)	54.5 (45 - 77)	-	51 (32 - 60)	45.5 (23 - 55)	-	0	0	_	0	0	_
Oct 2004	74 (64 - 85)	78.5 (65 - 88)	60 (43 - 77)	25 (3 - 35)	19 (12 - 35)	40 (23 - 57)	0 (0 - 33)	0 (0 - 6)	0	0	0	0
Nov 2004	67.5 (60 - 90)	81 (65 - 88)	72.5 (60 - 85)	9.5 (3 - 35)	12 (6 - 35)	13 (9 - 32)	12.5 (0 - 36)	6 (0 - 15)	14 (6 - 30)	0	0	0

APPENDIX K continued

Phenological traits for 10 procedural control mown Azorella selago *plants (8T) per altitude [median (range)].*

Date	**%Green**			**%Brown**			**%Budding**			**%Flowering**		
8T	Low	Mid	High	Low	Mid	High	Low	Mid	High	Low	Mid	High
Dec 2004	75 (62 - 84)	78 (70 - 89)	62 (56 - 76)	7 (2 - 20)	10.5 (5 - 30)	5.5 (3 - 32)	18 (3 - 36)	6 (0 - 20)	25 (6 - 38)	0	0	0 (0 - 11)
Jan 2005	75 (62 - 84)	78 (70 - 89)	62 (56 - 76)	7 (2 - 20)	10.5 (5 - 30)	6 (4 - 32)	0	0	0	18 (3 - 36)	6 (0 - 20)	27 (6 - 38)
Feb 2005	76 (62 - 84)	78.5 (70 - 90)	67 (56 - 75)	7 (2 - 20)	11 (5 - 29)	7 (4 - 30)	0	0	0	16.5 (2 - 33)	6 (0 - 20)	20.5 (10 - 38)
March 2005	81.5 (79 - 90)	83 (73 - 90)	70.5 (60 - 77)	18.5 (10 - 21)	12 (5 - 17)	17 (8 - 31)	0	0	0	0 (0 - 2)	3.5 (0 - 15)	11 (0 - 28)

Chapter 4: General conclusion

Climate has shown large, rapid changes over the past century, especially for high latitude ecosystems (IPCC, 2007). Significant changes in climate are reported for the Antarctic and sub-Antarctic Islands over the last 30 to 50 years (Walther et al., 2002). Predictions arising from these changes are already reported for the sub-Antarctic Marion Island (Smith and Steenkamp, 1990; Gremmen et al., 1998; Chown and Smith, 1993; Bergstrom and Chown, 1999; Smith et al., 2001; Smith, 2002; le Roux, 2004; le Roux et al., 2005; McGeoch et al., 2006). Species interactions are predicted to be sensitive to climate change, resulting in complex trophic interactions and community structures (Cramer, 1997; Convey, 2000; McGeoch et al., 2006). For example, *A. selago* and its dominant epiphyte, *A. magellanica* form an interaction that is predicted to be highly sensitive to climate change (le Roux et al. 2005; McGeoch et al. in press). However, the nature of the interaction between *A. magellanica* and *A. selago* had never been directly examined prior to this study, and the impact of the grass on the cushions remained poorly understood.

This study showed that microclimate temperature differed between the three study sites examined, with altitude and local topographic conditions being the main factors influencing cushion temperature (Chapter 2). Cushion size and height appeared to respond more to environmental heterogeneity, such as differences in age and structure, as expected (Pyšek and Liška, 1991; le Roux, 2004). Cushion vitality confirmed that *A. selago* thrives across a broad altitudinal range on Marion Island and across many sub-Antarctic Islands (Huntley, 1972; Gremmen, 1981; Smith et al., 2002; McGeoch et al., 2006). *Azorella selago* stem growth rate appeared to emphasize the importance of site specificity with no apparent spatial structure associated with altitude when estimating growth rate (le Roux and McGeoch, 2004; Nyakatya, 2006). Stems growing on a cushion surface area without epiphytic *A. magellanica* at the low altitude site had a higher growth rate, with an average of seven leaves per stem. The comparison of growth rate between exposed and shaded stems demonstrated a higher growth rate on exposed stems than the shaded ones. This suggests that shading by *A. magellanica* has a negative impact on *A. selago* stem growth rate.

Cushion morphology appeared to be more influenced by local habitat conditions, such as topography, as well as epiphyte cover. *Azorella selago* leaves were smaller at the mid

altitude site, with this attributed to the relatively low wind frequency at the mid altitude than at the high altitude site. Leaf size and leaf boundary layer resistance increases with wind speed, hence smaller leaves have a relatively thin boundary layer resulting in efficient heat transfer, whereas larger, thinner leaves provide a thick boundary layer with inefficiency in heat transfer away from the leaf (Bonan, 2002). Therefore, larger, thinner leaves at the high altitude site in this study could serve as a defense mechanism by the plant in the windier high altitude site on Marion Island. Mid altitude site leaves had a larger specific leaf area than all the other altitudes. This was accounted to the rainfall pattern experienced by *A. selago* leaves at the mid altitude site. One study on Marion Island attributes morphological variation in *A. selago* to moisture, light, and wind intensities (Nyakatya, 2006). The comparison between exposed and shaded specific leaf areas showed that the cushion surface area on which *A. magellanica* was growing and thus shaded by *A. magellanica*, produced leaves with larger specific areas, as expected for shaded plants (Salisbury and Ross, 1992; Havström et al. 1993; Michelson et al. 1996; Niklas, 1996; Cavender-Bares et al. 2000; Dormann and Woodin, 2002; le Roux et al., 2005).

The abundance and density of the dominant epiphyte, *A. magellanica* on *A. selago* was altitudinally related, as expected (le Roux, 2004; Nyakatya, 2006). This was the first study to quantify *A. magellanica* on and off *A. selago*, and it showed that the decline in *A. magellanica* number growing in fellfield matrix was more rapid off *A. selago* cushions than on cushions. These results therefore demonstrate a facilitative effect on *A. magellanica* by *A. selago* cushions at higher altitudes, with the abiotic environmental threshold for *A. magellanica* occurring at lower altitudes than it does for *A. selago*. *Azorella selago* phenology was also related to altitude, as well as to differences in temperature between the different altitude sites. This was demonstrated by cushion growth and flowering, which began earlier and was more rapid at the warmer, low altitude site, as expected and reported on a previous study on Marion Island (Nyakatya, 2006).

The experimental part of the research surprisingly showed that *A. selago* microclimate temperature was not affected by treatment application (Chapter 3). This could be attributed to an unclear temperature difference through monthly averages, but may be shown when measuring daily temperature fluctuations. Hence, the influence of grass on cushions may either have a cooling or buffering effect. The vegetative and reproductive performance of *A.*

selago was negatively affected by epiphytic *A. magellanica*. Shaded *A. selago* leaves remained brown, demonstrating a reduced photosynthetic surface area of *A. selago* as a result of the presence of the epiphyte, *A. magellanica*. The percentage of budding and flowering surface area on low grass density and procedural control weeded cushions was almost the same, demonstrating that simulating the action of weeding did not impose any damage to the plants. The low percentage cover of flower buds and flowers in cushions weeded in autumn and spring showed that the plants do not recover rapidly from the damage caused by epiphytic *A. magellanica* after its removal (at least not within 4 months at the low and mid altitude sites, and 5 months at the high altitude site for the cushions weeded in autumn; and one month for the cushions weeded in spring). A similar trend was observed for mown cushions for almost all vegetative and reproductive structures, suggesting a similar response of cushions to shading. Photosynthesis rates of plants decreases with photosynthetic area, hence plants exposed to less sunlight were expected to produce fewer flowers (Callaghan et al., 1992). Cushion vitality was also responsive to epiphyte load, with high vitality scores on low grass covered cushions than on high grass cushions. The effect of treatments on *A selago*, together with the direction of *A. magellanica* growing on and off *A. selago* cushions suggests that the vegetative and reproductive performance of *A. selago* and cushion vitality are likely to be negatively affected under climate change on Marion Island. This is attributed to the fact that grasses are generally reported to be favoured by climate change, due to their rapid turnover rates (Zhang and Welker, 1996; Dormann and Woodin, 2002). For example, an experimental study on *Agrostis curtisii* simulating warming showed that this grass species was positively related to increased temperature (Norton et al., 1999).

Baseline information and manipulative experiments used on this study show that *A. magellanica* competes with *A. selago*, whereas *A. selago* facilitates *A. magellanica*. This therefore suggests an asymmetric association since a positive association is only shown in one direction. This interaction has a negative effect on *A. selago*, since heavy epiphyte numbers impose negative effects on *A. selago* vegetative and reproductive performance, as well as cushion vitality (Chapter 3). Further colonization of *A. selago* cushions by epiphytic *A. magellanica* is therefore likely to impose negative effects on cushions by an increase in the percentage of brown, decrease in flower buds and flowering surface area of *A. selago* cushions, as well as decrease in vitality. Based on the results reported on this research, we

can therefore predict that further climate change will have negative indirect effects on *A. selago*. Hence, more research is needed to monitor this keystone species and the interaction with its dominant epiphyte, *A. magellanica*, as well as monitoring the altitudinal range of *A. magellanica* to detect early signs of possible upslope expansions in the altitudinal range of this species on Marion Island.

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